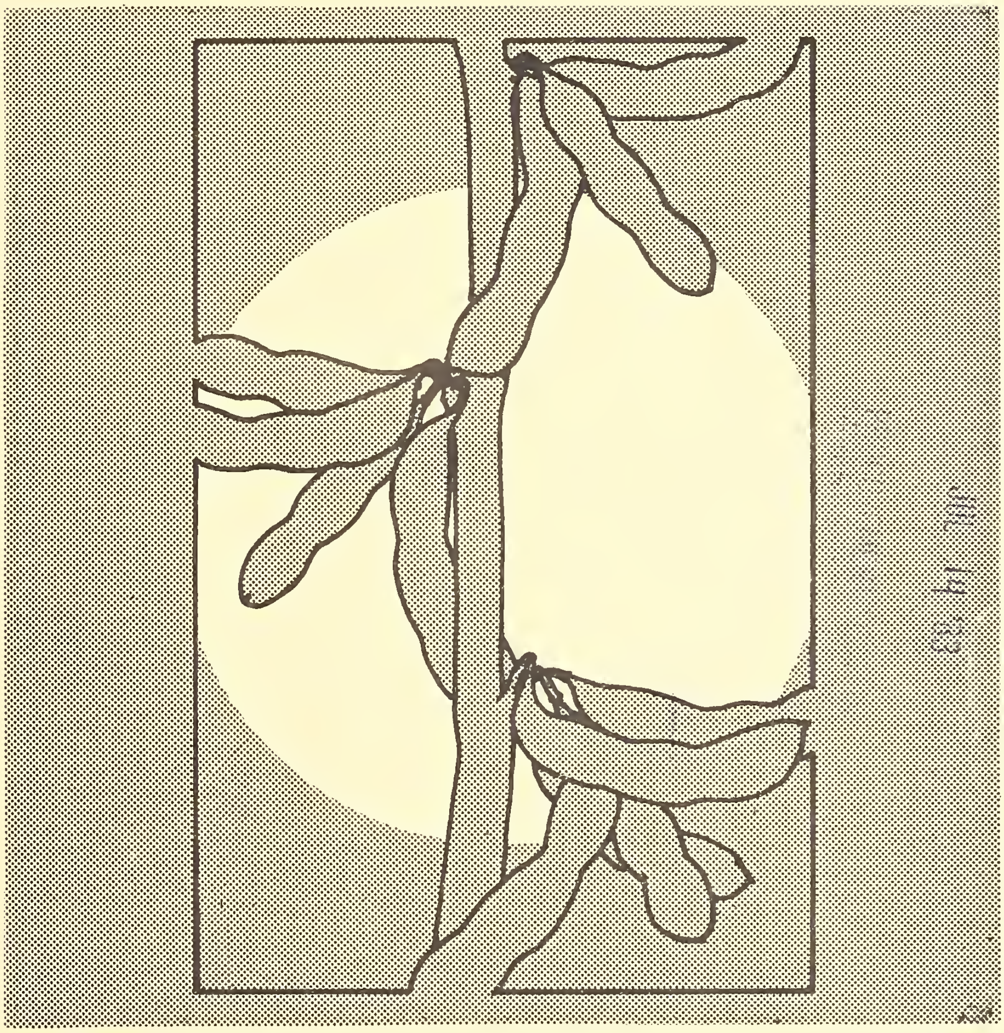
Soybean Genetics Newsletter



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The data presented here are not to be used in publications without the consent of the respective authors.

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I. FOREWORD

Being an industrious soybean research laboratory group, we haven't had time to celebrate this tenth anniversary of the birth of the Soybean Genetics Newsletter. We have, however, marked the occasion by putting together what seems to be the best issue yet. Each research note, we feel, is notable for its clear presentation of interesting and significant research work in the field of soybeans. Our thanks go to each of you, the authors, for making Volume 10 the best volume yet. Thanks also are due to Iowa State University graduate students from the Departments of Agronomy and Genetics, L. F. Chen, Lou Forrai, Peg Hatfield, Jeff Griffin, Bob Graybosch, Jeff Gwyn, and Randy Shoemaker, who "volunteered" many hours in preparing the literature citation section, and in proofreading; and to technicians Holly Heer and Susan Yost for their hours of editing and proofreading.

As we wrap up Volume 10, we are thinking ahead to Volume 11. A paragraph from the Soybean Genetics Committee report is of interest: "An updated list of soybean gene symbols is very much needed. Each committee member is asked to prepare such a list. Hopefully, this approach will result in the most complete list of symbols possible ...."

Your attention is called to the Announcements section of this issue. If you, as busy soybean scientists, can find the time (and funding), you would certainly benefit from attending at least one of the two upcoming international conferences about soybeans. This fall, in Japan, the first International Symposium on Soybean in Tropical and Subtropical Cropping Systems will be held. A year from coming August, Ames, Iowa, USA, will be the site of the World Soybean Research Conference-III. See the Announcements section for details on obtaining more information on these events.

Reid G. Palmer, editor

II. ANNOUNCEMENTS

The first International Symposium on soybean in Tropical and Subtropical Cropping Systems will be held in Tsukuba, Japan, September 26 through October 1, 1983, sponsored by the Asian Vegetable Research and Development Center and the Tropical Agricultural Research Center in cooperation with the International Soybean Program, the International Institute of Tropical Agriculture, the International Rice Research Institute and the Brazilian Agricultural Research Enterprise.

Stated goal of the symposium is

> "... to gain a better understanding ... and to coordinate future research on tropical soybean production, agricultural scientists, development officials and educators are cordially invited to participate in the first International Symposium on Soybean in Tropical and Subtropical Cropping Systems ... at the Tsukuba Science City, Japan. The symposium will: examine the present state of knowledge on soybean production under tropical and subtropical cropping systems, identify production limitations specific to the region and its cropping systems, establish a priority agenda for soybean improvement and cropping systems research, and develop strategies for the dissemination of information on these various topics."

Persons interested in attending the symposium are asked to contact Dr. S. Shanmugasundaram, AVRDC, P. O. Box 42, Shanhua, Tainan 741, Taiwan, or Dr. S. Motomura, Tropical Agricultural Research Center, Yatabe, Tsukuba, Ibaraki 305, Japan. Provide your name and address, and indicate whether you intend to present a paper and who will pay your expenses.

INTERNATIONAL SYMPOSIUM ON SOYBEAN IN TROPICAL AND SUBTROPICAL CROPPING SYSTEMS

• TSUKUBA JAPAN 1983 •

WORLD SOYBEAN RESEARCH CONFERENCE SCHEDULED FOR 1984

Ames, Iowa, USA, will be the site of the World Soybean Research Conference-III, August 12-17, 1984.

Iowa State University is pleased to invited all soybean scientists to attend World Soybean Research Conference-III. The conference will provide an opportunity to discuss recent advances in research on soybean production, marketing, and utilization. Scientists in all disciplines of soybean research from throughout the world are invited to attend.

Information about the conference may be obtained by writing

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World
Soybean
Research Conference—III

1984

STADLER GENETICS SYMPOSIUM: March 19-21, 1984

"Gene Manipulation in Plant Improvement"

The sixteenth Stadler Genetics Symposium will be held in Columbia, MO the week of March 19, 1984. The Symposium will focus on gene manipulation in plant improvement through 25 presentations by internationally recognized plant scientists. Contributed posters are welcome. Invited speakers include: Burton of Georgia, Duvick of Iowa, Rasmusson of Minnesota, Evans of Australia, Baker of Canada, Hooker of Missouri, Cocking of United Kingdom, Simmonds of United Kingdom, Dewey of Maryland, Collins of Kentucky, Kimber of Missouri, Sears of Missouri, Riley of United Kingdom, Baenziger of Maryland, Bennett of United Kingdom, Rajaram of Mexico, Borlaug of Mexico, Rochaix of Switzerland, Long of California, Meredith of California, Beachy of Missouri, Orton of Colorado, Appels of Australia, Bedbrook of California, and Khush of Philippines.

A sample of the topics to be considered at the Symposium are: Conventional Plant Breeding, Chromosome Manipulation, Gene Expression in Plants, DNA Manipulation, Use of DNA Cloned in Bacteria, Cell and Tissue Culture, Genetic Manipulation of Nitrogen Fixation, Pathological Framework of Plant Breeding, Quantitative Genetic Principles.

For registration information please contact Dr. J. P. Gustafson, 208 Curtis Hall, Department of Agronomy, University of Missouri, Columbia, MO 65211. 316/882-7318.

New Officers of the Executive Committee of the Commercial Plant Breeders Association

John Schillinger - Chairman
Asgrow Seed Company
634 E. Lincolnway
Ames, IA 50010
(515) 232-7170

Josh Stanton - Vice Chairman
Coker Pedigreed Seed Company
Box 340
Hartsville, SC 29550
(803) 332-8151

Jimmy Barber - Sec./Treas.
NAPB
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West Memphis, AR 72301
(501) 735-6537

III. USDA SOYBEAN GERMPLASM COLLECTION REPORT

The following table summarizes the new additions to the Germplasm Collection grown at Urbana, Illinois, in 1982:

Country of Origin	2nd Year	New
China	43	118
S. Korea	223	
Japan	4	1
Sweden		2
Total	270	121
Wild Soybean (China)	30	26

Strains become available for distribution after the second year and so the 270 above increase the total FC and PI strains at Urbana to 6792 and the 30 wild soybeans increase the total number of *G. soja* to 590. We have had no major acquisitions from Chinese germplasm collections but, as the figures above indicate, we are getting an appreciable number of varieties each year including some wild soybeans. These are mostly brought in by various agricultural travelers, both American and Chinese. These Chinese introductions are about evenly distributed from Maturity 000 to IV. Dr. Shin Han Kwon has been making further collections of native South Korean germplasm and has again generously shared them with us (Maturity III and IV to Urbana, V and VI to Stoneville).

Seed requests for more than 30,000 packets were filled and sent out from Urbana during 1982.

The status of the Southern Germplasm Collection at Stoneville, Mississippi, is summarized by Maturity Group below:

	Number of entries		
	to 1980	Additions after 1980	Total as of 12/82
V	1369	134	1503
VI	421	45	466
VII	314	16	330
VIII	266	19	285
IX	109	15	124
X	136	12	148
Total	2615	141	2856

Agronomic data are available on all 2856 strains and, for most of them, data are available on Race 1 Phytophthora response, bacterial pustule response, and protein, oil, and fatty acid composition. Seed requests from 14 countries and 30 states for 9500 entries were filled and sent from Stoneville during 1982. Group VI germplasm was grown at Stoneville in 1982 and Group VII, VIII, and IX will be grown in 1983.

R. L. Bernard
R. L. Nelson
E. E. Hartwig
C. Edwards

IV. SOYBEAN GENETICS COMMITTEE

Minutes of Meeting

The Soybean Genetics Committee met Monday, February 21, 1983, at the Airport Hilton, Memphis, Tennessee. This meeting was in conjunction with the annual meeting of the Soybean Breeders Workshop.

Committee members in attendance were R. L. Bernard, H. R. Boerma, T. E. Devine, E. T. Gritton, H. H. Hadley, T. C. Kilen, C. Newell, J. H. Orf. Also present were J. R. Wilcox and H. D. Voldeng. Drs. Boerma and Devine have been elected to new three-year terms on the committee, replacing Drs. Gritton and Newell, whose terms expire at the close of this meeting. Present committee members and the expiration of their terms are as follows:

R. L. Bernard, USDA, Ex Officio
(Curator of soybean genetics collection)
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Dr. Orf was elected chairman of the committee for the coming year, so manuscripts should now be submitted to him.

The number of manuscripts received for review by the committee increased to 13 from 4 during the previous year. Persons who are not members of the committee will be asked to review manuscripts when their area of expertise is needed, and to spread the workload.

It was moved by Devine, seconded by Hadley, that the curator of the soybean genetics collection be made an ex officio member of the Soybean Genetics Committee with full voting rights. Motion passed. Dr. Bernard will thus become a member.

Last year, this committee had proposed that a new committee, in addition to and distinct from the SGC, be established for communication of genetic information, work in progress, researchers, etc. We suggest that a meeting be announced at the World Soybean Research Conference to be held at Ames, Iowa, August 12-17, 1984, and all persons interested in such a committee be invited to meet and discuss the possible formation of such a committee.

An updated list of soybean gene symbols is very much needed. Each committee member is asked to prepare such a list. Hopefully, this approach will result in the most complete list of symbols possible. A current list will be needed soon as the monograph *Soybeans: Improvement, Production and Uses* is updated.

The committee discussed the review of manuscripts and assignment of gene symbols. The final choice is up to the researcher involved provided the symbol has not previously been assigned. We do hope the rules as set forth in the Soybean Genetics Newsletter will be followed.

Submitted by:

Earl T. Gritton, Past Chairman
Soybean Genetics Committee

V. RESEARCH NOTES

AGRICULTURE CANADA
Research Station
Harrow, Ontario, Canada

Canada

1) Tolerance/resistance to soybean mosaic virus

A natural epiphytotic of soybean mosaic virus (SMV) occurred at the Harrow Station in 1976. The disease, which was noted in early July, reduced plant growth. Advanced lines from 'Corsoy' x 'Chippewa 64' were being tested in the field in relation to their flavonol glycoside classification. Plants were rated for severity of leaf symptoms and seeds were rated for mottling.

The parents differed in degree of leaf symptoms and in seedcoat mottling; there were differences among the lines also (Table 1). Although the gray-pubescent Corsoy had a higher mottling rating than the brown-pubescent Chippewa 64, the *TT* lines had a higher average rating than *tt*. Wilcox and Laviolette (1968) reported greater mottling for *T* vs. *t*.

Table 1. Test results from Corsoy (*t*) x Chippewa 64 (*T*)

		Ratings (1 =none; 9 = severe)		
	n	Min.	Average	Max.
		Leaf symptoms Aug. 4, 1976		
Corsoy	4	4.0	5.4 a	7.0
Chippewa 64	4	1.0	1.5 b	2.0
Lines	48	1.0	2.8	6.2
		Seedcoat mottling		
Corsoy	4	1.0	2.7 o	4.0
Chippewa 64	4	1.0	1.9 p	3.0
Lines	48	1.0	3.0	5.8
T	24	1.5	4.1 x	5.8
t	24	1.0	2.0 y	5.0

n = number in each of 4 replicates.

a, b; o, p; x, y significant differences for each pair, P = 0.01.

Broad-sense heritability was 92% for leaf ratings and 97% for seedcoat ratings. However, ratings for mottling were not closely correlated with the leaf ratings (r = +0.52**; P = 0.01). The 48 lines were separated into three equal groups of those with the lowest, intermediate, and highest mean ratings for leaf symptoms. The three groups differed (P = 0.01) for yield in 1976 but not in 1974 (a year when SMV was not a problem). Although direct comparisons of magnitude cannot be made between the years, the relative performance of the groups can be assessed. In 1976, the groups with lowest, intermediate, and highest ratings yielded 84, 69, and 58% of their yield in 1974, which indicates that some of the lines were more tolerant to SMV than others.

In addition, 'Raiden' and some of its progeny were free of leaf symptoms and seedcoat mottling in 1976, which suggested resistance to the virus. The resistance was attributed to a single dominant gene. Kiihl and Hartwig (1979) have reported an *Rsv* gene for SMV resistance; the gene from Raiden is different from it (Buzzell and Tu, unpublished) and is not linked to a gene (probably Rps_1^c) for phytophthora resistance (Table 2).

Table 2. Test results from OX613 (rsv_2 rps) x OX615 (Rsv_2 Rps)

Genes	a	b	c	d	Sum	R%	SE	Phase
Rsv_2 rsv_2 Rps rps*	54	12	20	7	93	43.7	7.2	C

*Probably Rps_1^c.

Rsv_2 (OX615) and rsv_2 (OX615-S) isolines derived from an F_4 plant of 'Harcor' x OX315 (Harcor x Raiden) were tested for yield in 1978 and 1979 in a field where SMV was prevalent. The susceptible isoline yielded 19% less than the resistant isoline. OX615 was free of leaf symptoms, was taller, and had no seedcoat mottling. Leaf symptoms were not severe on OX615-S but maturity was delayed; seedcoat mottling was rated as 2.7 (1 = none; 5 = considerable).

References

Kiihl, R. A. S. and E. E. Hartwig. 1979. Inheritance of reaction to soybean mosaic virus in soybeans. Crop Sci. 19:372-375.

Wilcox, J. R. and F. A. Laviolette. 1968. Seedcoat mottling response of soybean genotypes to infection with soybean mosaic virus. Phytopathology 58:1446-1447.

100 R. I. Buzzell

345 Soybean cultivar response to manganese [1, 2]

Manganese deficiency of soybeans, *Glycine max* (L.) Merr., commonly occurs in southwestern Ontario. Observation of soybean fields indicated that cultivars differed in degree of Mn-deficiency symptoms. To test this observation, 'Harosoy 63' and 'Harman' were grown in 3-replicate tests at six locations in 1963; and, in 1964 and 1965, these cultivars were grown along with 'Hawkeye 63' and 'Lindarin 63' in 4-replicate tests at one location. The soils were Brookston clay with phosphate-extractable Mn (Hoff and Mederski, 1958) between 2.7 and 4.8 ppm. Soil pH ranged from 6.0 to 6.7 and the acid soluble plus absorbed phosphorus (Bray and Kurtz, 1945) ranged from 56 to 124 ppm. Manganese sulfate was applied at the recommended rate of 9 kg/ha as a foliar spray around the first of July for comparison with unsprayed plots. We sampled newly expanded upper leaves 3 to 4 weeks after spraying (i.e., during pod set) and determined Mn content colorimetrically. Bean yield was measured. Mn content of the 1965 seed was determined.

Jones (1967), using samples taken prior to pod set, arrived at the following categories for soybean leaf Mn: 14 ppm and less as deficient, 15 to 20 ppm as low, and 21 to 100 ppm as sufficient. Using Jones' classification with the reservation that our leaf Mn values may be lower than would have been obtained prior to pod set, our results (Table 1) show that there are differences among soybean cultivars in Mn nutrition. Harman and Hawkeye 63 are more likely to be in the deficient category than are Harosoy 63 and Lindarin 63. Also, Harman and Hawkeye 63 are more likely to show yield responses in the low category than are Harosoy 63 and Lindarin 63. Cox (1968) indicated that 20 ppm of Mn in the leaf and the seed was the critical level for Mn deficiency. The untreated Harman and Hawkeye 63 averaged 2 ppm less Mn in the seeds than in the leaves, whereas Harosoy 63 and Lindarin 63 averaged 4 ppm less.

Table 1. Soybean cultivar response to managaese

	Mn++ ppm in leaves			Bean yield (kg/ha)		
Cultivar	0		Mn	0		Mn
			1963			
Harosoy 63	17		18	1650		1720
Harman	12	*	15	1530	*	1770
			1964			
Harosoy 63	14	*	17	2170	*	2800
Harman	13	*	16	1580	*	2410
Hawkeye 63	10	*	16	1950	*	2770
Lindarin 63	14		16	1650	*	2410
			1965			
Harosoy 63	19		22	2500		2470
Harman	18		22	1800	*	2670
Hawkeye 63	17		22	1930	*	2720
Lindarin 63	19		22	2020		2300

*Treated differed significantly (P = 0.05) from untreated.

References

Bray, R. H. and L. W. Kurtz. 1945. Determination of total, organic and available forms of phosphorus in soils. Soil Sci. 59:39-45.

Cox, F. R. 1968. Development of a yield response prediction and manganese soil test interpretation for soybeans. Agron. J. 60:521-524.

Hoff, D. J. and H. J. Mederski. 1958. The chemical estimation of plant available soil manganese. Soil Sci. Soc. Amer. Proc. 22:129-136.

Jones, J. B., Jr. 1967. Interpretation of plant analysis for several agronomic crops. pp. 49-58. In Soil testing and plant analysis, Part II Plant analysis. Soil Science Society of America, Inc., Madison.

100 R. I. Buzzell
W. I. Findlay

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India

1) 845 <u>Dry matter yield and branching ability as selection parameters in soybean</u> [22].

During the process of varietal development, a large number of new breeding lines of soybean (PK-series) generated through hybridization and selection are evaluated each year at this centre and elite ones (about 40) are maintained for further use. A brief report of some of these lines has been published (Ram et al., 1982). A path-coefficient analysis using typical yield components and the physiological parameters of yield, viz. dry matter yield (above ground parts), harvest index and seed yield efficiency, was carried out in 50 soybean genotypes (40 new PK-series lines + 10 parental/check cultivars) evaluated during rainy season 1980. The results are summarized in Table 1.

Table 1. Phenotypic, genotypic correlations and corresponding direct effects of 16 quantitative traits with seed yield in soybean

Characters	Phenotypic		Genotypic	
	Correlation	Direct effect	Correlation	Direct effect
Days to flower	-0.210	-0.134	-0.282	2.339
Days from flowering to maturity	0.354*	-0.078	0.515	0.258
Days to maturity	0.180	0.029	0.215	0.081
Basal-node height (cm)	-0.016	-0.028	-0.000	0.412
Basal-pod height (cm)	0.022	-0.008	-0.325	-0.898
Leaflet width (cm)	0.331*	0.003	0.565	-1.109
Leaflet length (cm)	0.353*	0.057	0.611	0.523
Plant height (cm)	-0.294*	-0.000	-0.393	1.186
Number of primary branches per plant	0.443**	0.058	0.436	0.479
Number of pods/plant	-0.128	0.230	-0.307	0.136
Number of seeds/pod	-0.210	-0.021	-0.396	-1.550
Number of nodes/plant	-0.110	-0.015	-0.281	-3.727
100-seed weight (g)	0.372**	0.026	0.513	-1.609
Dry-matter weight/plant (g)	0.639**	0.763	1.048	1.171
Harvest index	0.557**	0.665	1.046	0.301
Seed yield efficiency	0.491**	0.073	1.937	-0.017

*,** Significant at 5 and 1 percent probability, respectively.

The traits having significant positive phenotypic correlations with seed yield, and also supported by the genotypic correlations, were days from flowering to maturity, leaflet width, leaflet length, number of primary branches, 100-seed weight, dry-matter weight, harvest index, and seed yield efficiency. Plant height was negatively correlated with seed yield.

The physiological parameters of seed yield, viz. harvest index (seed yield/above ground plant dry weight) and seed yield efficiency (seed weight/above ground nonseed dry weight), are directly related to dry-matter yield which has shown positive correlation with seed yield. Joshi and Smith (1978) have also suggested that selection based on unthreshed weight should be helpful in improving soybean yield. The significance of dry-matter yield, harvest index, seed yield efficiency, number of primary branches, leaflet length, and 100-seed weight in determining seed yield was obvious through path-coefficient analysis also as these components had substantial direct effect upon seed yield both at phenotypic and genotypic level.

Breeding implications: In light of these results and practical feasibility during the process of selection, it is suggested that dry-matter weight and number of primary branches/plant should get priority for yield improvement. Dry-matter weight proved to be of further importance since it had high genotypic correlation with harvest index ($r_g = 1.452$) and seed yield efficiency ($r_g = 3.085$) which, in turn, had strong association with seed yield. Dry-matter weight had another advantage in that it was positively correlated with number of primary branches/plant ($r_p = 0.378$, $r_g = 0.390$), which itself was observed to be an important seed yield determinant.

Branching ability should also be considered as an important trait while selecting varieties of high yield potential for tropical and subtropical environment. High branching varieties may have the ability to compensate for poor plant stand by producing more branches/plant under less plant competition. Singh (1976) has suggested that the plants with intermediate height (75-90 cm), with 8-10 branches, having narrow leaves and seed size in the range of 12-15 g/100 seeds seem to be the ideal plant types for tropical regions. Most of the breeding lines studied by us were in this branching (8-10 branches/plant) range. However, our observations do not support the advantages of narrow leaflets to increase seed yield in soybean. Mandl and Buss (1981) evaluated the effect of leaflet shape on the agronomic performance of soybean lines by using narrow and broad leaflet isolines with varied genetic backgrounds. Analysis over years showed that the narrow leaflet lines were significantly shorter and had smaller seeds. Lodging scores were similar for both the leaflet types. They concluded that narrow leaflet trait offers neither a yield advantage nor disadvantage compared with the broad leaflet trait.

Thus, in conclusion, we suggest that dry matter yield, branching ability and preferably broader leaflets should be the selection parameters in soybean in the tropics.

References

Joshi, J. M. and P. E. Smith. 1978. Correlated response of certain plant traits with seed yield in soybeans. Soybean Genet. Newsl. 5:62-65.

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Ram, H. H., V. D. Verma, K. Singh and Pushpendra. 1982. New breeding lines of soybean developed at Pantnagar. Soybean Genet. Newsl. 9:39-42.

Singh, B. B. 1976. Breeding soybean varieties for the tropics. In: Proc. Conf. Asia and Oceania, Thailand. pp. 11-17.

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Hari Har Ram

100

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1. Cyst nematode screening methods, indexes and their uses

The threat of the soybean cyst nematode, *Heterodera glycines* Ichinohe, to soybean in the North Central States of the United States is continuing and will likely increase in severity with time. Southern states have dealt with this pest for a number of years and states with large acreages have designed screening methods to detect and test for nematode resistance.

This report describes the screening method used at the Northeast Research and Extension Center, Keiser, Arkansas. There have been no cyst nematodes detected at Keiser (NEREC) and, because of this, it was decided by the cooperative team members not to screen for cyst nematode on soybean lines, bulks and other material at Keiser. We, therefore, have been sending our material to Arkansas State University at Jonesboro, AR, and to the University of Arkansas at Fayetteville, AR, for screening purposes.

At Jonesboro, personnel have collected soil from the "hottest" areas available with which to screen soybeans. Soil has been collected from an area in Missouri and other areas that are reported to contain a mixture of races 3, 4 and "5". Race "5" has been reported to infect 'Bedford', a maturity group V cultivar with resistance to races 3 and 4 of cyst nematode. At Jonesboro, no direct attempt has been made to screen for specific races using specific soybean cultivars or Plant Introductions (PIs) to separate the cyst nematode races.

At Fayetteville, Dr. Riggs has developed a technique, over a number of years, to separate and screen soybean breeding material for the specific races of cyst nematode. The Fayetteville program tests soybean material against 'Lee' cultivar - the susceptible commercial check, 'Pickett' cultivar - an older cultivar resistant to race 3, 'Peking', Bedford, PI 88788, PI 90763J and PI 90763R. Cyst counts taken from the roots of Lee cultivar are taken as 100% susceptible and the average counts taken from the tester lines (i.e., Pickett, Bedford, Peking, PI 88788, PI 90763J and PI 90763R) and the soybean material to be screened are divided by the average counts from Lee cultivar to obtain a susceptibility index relative to Lee, a standard soybean type in the southern U.S.

At Jonesboro, six frequency classes have been established (0, 1, 2, 3, 4, 5) for visual screening of each tested pot of soybean. 0 class represents no cysts present on the root ball, class 1 = 1 to 5 cysts present, class 2 = 6 to 10 cysts read, class 3 = 11 to 20 cysts read, class 4 = 21 to 30 cysts observed and class 5 = 31 or more cysts present on the root ball.

We have taken the Fayetteville Lee cultivar race-specific susceptibility indexes and the Jonesboro field screening class observation and combined them to give a rather complete picture of the susceptibility or resistance (or tolerance) of each line or bulk screened. A plant breeder, by using these procedures, can detect resistance or susceptibility to specific races and to field populations of cyst nematode that threaten soybean producers in commercial soybean growing areas. We have included appropriate checks after each 20 or 30 entries and do not identify the entries until the screening procedures have been completed. Computer assistance would speed the computation

of the Jonesboro data to obtain the "resistance index." If raw data were keypunched into a programmed system for the indexes, the operation would be greatly enhanced.

An example of specific data is given in Table 1 using Bedford and experimental lines to demonstrate how the indexes are obtained. By subtracting the Fayetteville indexes from 100, a "resistance index" would be obtained rather than a "Lee susceptibility index."

By using the above procedures, researchers may obtain data that will lead to new approaches for solving the mechanism of resistance of such lines as PI 90763, PI 88788 and Peking. The resistance is likely to be a combination of biochemical and biophysical factors and will have to be bred into soybean. If the resistance mechanism is purely biochemical, a compound might be synthesized to give "field resistance" and breeders could concentrate on yield factors. However, the resistance complex probably will involve both chemical and physical structures of the root not yet defined.

Possible current uses of the combination of the specific race screen and the "field screen" include the following:

1) Reselection within Bedford to obtain higher resistance levels than that currently obtained and possibly reducing the amount of black seed and "bleeding hilas" now found in Bedford.

2) Achieve more thorough resistance levels to known races of cyst (1) and to the "hottest," newest, most damaging populations present within specific field areas (2).

3) Compare efficacy of "race screening" versus "field screening" methods and to compare both methods to the "petri dish" technique currently in use. Our concern with the "petri dish" technique would be whether or not the infection at days 3 to 10 in the petri dish would simulate the actual infection ontogeny that occurs in the field. That is, do "petri dish" techniques represent, accurately, when economic infection levels occur in the field and, if not, why not?

4) Race changes can be observed, particularly from the field soil used for the "field resistance" screen and reselection for new specific races would then be appropriate.

5) Detection of the effect of the "Arkansas rotation" recommendations on specific races can be monitored easily and, if changes seem appropriate in either the host soybean alleles for resistance or the crop rotation recommendations, they could be done.

6) New research opportunities will appear when plant pathologists/nematologists and plant breeders are involved in a team effort required by this type of program. Biological control of the *Heterodera* spp. and other control methodologies will be forthcoming but require a monitoring program as described above.

7) Improved explanation of the genetics of nematode resistance should be facilitated since better control of "field" populations and individual races would be available.

Table 1. Soybean cyst nematode data obtained from Fayetteville and Jonesboro, AR, screening locations

Fayetteville - (race-specific screen)

Entry No.	Race 3 replications 1	2	3	4	5	Ave.	Susceptibility Index	Race 4 replications 1	2	3	4	5	Ave.	Susceptibility Index
1 (Lee)	200	460	480	208	320	334	100.0	320	1280	960	720	1080	1072	100.0
2 (Bedford)	1	6	10	13	10	8	2.4	40	60	200	280	--	145	13.5
3	15	4	12	20	38	18	5.4	200	72	144	168	124	142	13.2
4	5	24	160	8	8	41	12.3	144	132	100	84	104	113	10.5
5	22	4	2	0	200	46	13.8	120	92	172	104	128	123	11.5

Jonesboro - (Field resistance screen)

Entry No.	Surviving plant number	Susceptibility class 0	1	2	3	4	5	Infection class "points" assigned 0	1	2	3	4	5	(A) Possible 100% infection*	(B) Total actual points	(C) Potential infection index - % (B)÷(A)x100)	Resistance index 100-(C)
1 (Lee)	N/A[a]	-	-	-	-	-	-	-	-	-	-	-	-	--	--	--	--
2 (Bedford)	8	1	4	3	0	0	0	0	4	6	0	0	0	40	10	25	75
3	4	0	0	4	0	0	0	0	0	8	0	0	0	20	8	40	60
4	2	0	0	2	0	0	0	0	0	4	0	0	0	10	4	40	60
5	10	0	0	7	3	0	0	0	0	14	9	0	0	50	23	46	54

*Plant number x 5 (worst infection level).

[a]N/A = Not applicable.

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1) Variation in water-absorbing capacity of soybean seeds

Water-absorbing capacity (WAC) of soybean seeds is an important factor in the efficient production of soy food products in Japan and other Asiatic countries. Variation in WAC, therefore, should interest persons in the USA concerned with exporting soybeans to these countries. Soybeans vary in WAC depending upon soaking conditions (e.g., temperature and length of soaking time), initial moisture content of the seed, quality of the seed coat, and probably genotype. We are interested in learning the relative importance of genotype.

We have screened 1,271 soybean genotypes (mostly plant introductions) from maturity groups I, II, III, and IV grown by Dr. R. L. Nelson at Urbana, Illinois, in 1980. We estimated WAC by soaking 10 g of apparently healthy and intact seeds in 30 ml of distilled water for 10 hours at room temperature. This method is not as refined as the more precise but more time-consuming method developed by Cheng (1981). It is approximately the same as the shorter method described by Cheng for screening and ranking large numbers of genotypes and is expressed by the following formula:

$$\text{WAC} = \frac{(\text{weight of soaked seeds} - \text{weight of dry seeds})}{\text{weight of dry seeds}} \times 100$$

The moisture content of the "dry seeds" (before soaking) was not measured. Possible variations in initial water content might reduce the accuracy of our screening in ranking genotypes.

Our estimates of WAC ranged from 18.1 to 155.8 when all 1,271 genotypes were considered (Table 1). Low estimates of WAC were associated with high percentages of hard seed. Genotypes with high WAC estimates had few or no hard seeds. Variations in frequency of hard seeds, however, did not account for all the variation in WAC. Even within populations of samples having only soft seeds, estimates of WAC ranged from 117.0 to 148.8 in genotypes from maturity group I and 116.3 to 155.8 in those from maturity group IV. The range was even greater in group II (90.6) and in group III (50.0).

Lines differing widely in WAC have been crossed to generate F_2 hybrid populations for inheritance studies. Tests of 1982-grown materials are being run to determine the importance of determining initial moisture content of seeds and the effects of years on estimation of WAC.

Reference

Cheng, Shui-Ho. 1983. Variation in some soybean (*Glycine max*) [L.] Merr.) seed characteristics of possible importance in soybean processing. M.S. thesis. University of Illinois, Urbana-Champaign, Illinois, USA 61801.

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Table 1. Variation in frequency of hard seeds and in water absorbing capacity in soybean germplasm (1980 seeds)

Maturity group	Number of genotypes tested			Water absorbing capacity (WAC) among:				
				All genotypes			Genotypes with no hard seeds	
	Total	With no hard seeds	With hard seeds	Low	High	Mean	Low	High
I	217	52	165	18.1	148.8	115.9	117.0	148.8
II	209	72	137	38.4	152.5	114.1	61.9	152.5
III	307	154	153	25.2	150.4	129.1	93.4	143.4
IV	538	282	256	47.3	115.8	133.8	116.3	155.8
	1,271	560	711					

#45 2) Studies in polyploidy in soybeans: A simple and effective colchicine technique of chromosome doubling for soybean (*Glycine max* (L.) Merr.) and its wild relatives.

Tang and Loo (1940) first reported the induction of tetraploid soybeans by soaking day-old seedlings in 0.05 to 0.1% colchicine solution for 24 or 48 h. Oinuma (1952) obtained tetraploids by soaking dry soybean seeds in 0.1% colchicine solution for 24, 48 and 72 h. His results showed that the survival of resulting plants was poor. Sen and Vidyabhusan (1960) reported that polyploidy could be induced either by soaking the seeds in colchicine solution or treating the apical bud of the germinating seedling by a cotton wad saturated with colchicine solution, but they obtained few polyploids with these methods. A more successful colchicine technique for inducing tetraploidy in soybeans was reported by Tang and Lin (1963). They found that treating the apical buds with 0.3% colchicine-lanolin mixture gave about 47% success. Treatment with a colchicine-lanolin mixture, however, may cause continued induction of chromosome doubling because the lanolin mixture can last much longer than an aqueous solution of colchicine. This may reduce the frequency of recovered tetraploids. In the wild relatives of soybean, Palmer and Hadley (1968) obtained tetraploid plants of *Glycine tomentella* (formerly *Glycine tomentosa*) by applying warm 0.5% colchicine-lanolin paste to the axillary buds at the base of young cotyledons just before the cotyledons spread open. We have found the procedures described below to be quite effective in doubling chromosome numbers of several cultivars of *G. max* as well as different wild soybean genotypes. Detailed statistics have not been determined, but the degree of success has been well over 50%.

Procedure 1 - for Subgenus *Soja*, i.e., *Glycine max* and *Glycine soja*

1) Germinate the seeds in pots. When the two single leaves of resulting seedlings spread completely open and the apical bud grows to about 0.5 cm long, but no longer, wrap the three portions of meristematic tissue (i.e., the apical portion plus the axillary portions at the base of both single leaves) with cotton. Completely saturate the resulting cotton wad with a 0.1% aqueous solution of colchicine twice a day by using a dropper. A total of 3 applications is enough, e.g., treatment can be done once in the morning and once in the afternoon of the first day and once in the morning of the next day. The time interval between treatments on the first day should be longer than 4 h.

2) On the third day, after the colchicine treatment is finished, remove the cotton from the wrapped plants. Care for the treated plants in the regular way. After 4 to 6 days, the axillary buds at the base of cotyledons will grow out. Be sure to remove them as soon as they appear.

3) When polyploid buds grow out from the three treated parts of the seedling, check them visually and remove any new, rapidly growing shoots that look like the original plant morphologically and are probably diploid.

Procedure 2 - for chromosome doubling of Subgenus *Glycine* such as *Glycine tabacina*, *Glycine tomentella*, etc., and their hybrids either among themselves or with Subgenus *Soja*

1) Seedlings of the Subgenus *Glycine* are very tiny. Furthermore, treatment of one meristematic region of these perennial types simply arrests growth in that area of the plant while growth continues in other areas. There is no forcing of treated tissue to renew growth necessary for recovery of cells with the doubled chromosome number. Thus, a straightforward grafting technique as described by Newell and Hymowitz (1979) is used first to graft the scion of the wild soybean onto stock of the cultivated soybean before colchicine treatment.

2) About 2 to 3 weeks later, when the scion has grown out after grafting, cut out the apical shoot as the second leaf of the wild soybean scion spreads open and the axillary bud grows up about 0.5 cm (no longer than 0.5 cm). Do the same wrapping, treating, and caring work as in Procedure 1 for the Subgenus *Soja*.

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3) Studies in polyploidy in soybeans: Cytologically identified tetraploid *Glycine max* and *Glycine soja* and a preliminary observation on seed yields of tetraploid 'Williams' plants.

A partial list of cytologically identified tetraploid *Glycine max* and *Glycine soja* genotypes is presented in Table 1. Some of these genotypes apparently are new at the tetraploid level.

Sixty-three (63) single plants of tetraploid Williams were harvested on the Agronomy South Farm at Urbana in 1982. Five single plants of diploid Williams grown on the same experimental field were sampled as a check. The distribution of single plant seed yield of the tetraploid Williams ranged from 3.7 to 79.6 g per plant (Table 2). Seed yields of diploid Williams

varied from 33.6 to 69.8 g per plant and averaged 52.1 g. Some of the tetraploid plants were comparable to the diploid plants. Tremendous variation in fertility of the tetraploid plants was observed.

Table 1. Tetraploid *Glycine max* and *Glycine soja* genotypes

Glycine max	Chromosome no.	*Glycine max*	Chromosome no.
	4n=		4n=
Williams	80	Blackhawk	80
Beeson	80	Lincoln	80
Wells	80	Harman	80
Century	80	Dunfield	80
Amcor	80	Manchukota	80
Gnome	80	Dunn	80
Harosoy	80	*Glycine soja*	80
Richland	80	PI 378702	80
Chippewa	80		

Table 2. Distribution of seed yields of 63 tetraploid Williams plants

Seed yield/plant (g)	Number of plants
1-10	7
11-20	16
21-30	22
31-40	9
41-50	7
51-60	0
61-70	1
> 70	1

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4) Evaluation of chlorophyll-retention near-isogenic lines of soybeans

The phenomenon of chlorophyll retention in soybeans [*Glycine max* (L.) Merrill] is worthy of investigation for several different reasons: 1) it may have a physiological impact upon yield, 2) it may be useful in helping to explain the process of senescence, and 3) it causes production of green seeds, which may differ from normal yellow seeds in chemical composition, size, germination, nutritional qualities, and/or potential usefulness as vegetable types.

Different genetic systems control the retention of chlorophyll, which results in green seed color (1). Ten near-isogenic lines in both 'Clark' and 'Harosoy' backgrounds are currently being studied to characterize and compare the different chlorophyll-retention types with their normal counterparts. Differences among lines involve two types of cytoplasm and variations at three nuclear loci (Table 1). All lines, with the exception of the "normal" forms, were derived by the backcross method by R. L. Bernard, from whom our material was obtained.

Agronomic as well as physiological traits were determined for all genotypes, and some preliminary results from our first year's evaluation (1981) are reported here.

Table 1. Listing of soybean isolines of 'Clark' (C) and 'Harosoy' (H) background

Designation	Genetic constitution	Phenotypes	
		Seedcoat	Embryo
C-"normal"	$gg\text{-}D_1D_1D_2D_2$	Yellow	Yellow
C-Gd_1	$GG\text{-}d_1d_1D_2D_2$	Green	Yellow
C-Gd_2	$GG\text{-}D_1D_1d_2d_2$	Green	Yellow
C-Gd_1d_2	$GG\text{-}d_1d_1d_2d_2$	Green	Green
C-Cyt *G*	cytoplasmic	Green	Green
H-"normal"	$gg\text{-}D_1D_1D_2D_2$	Yellow	Yellow
H-Gd_1	$GG\text{-}d_1d_1D_2D_2$	Green	Yellow
H-Gd_2	$GG\text{-}D_1D_1d_2d_2$	Green	Yellow
H-Gd_1d_2	$GG\text{-}d_1d_1d_2d_2$	Green	Green
H-Cyt *G*	cytoplasmic	Green	Green

Physiological traits: Five leaf samplings were made every 10 days from 20 to 60 days after flowering in Harosoy lines, and from 30 to 70 days after flowering in Clark lines. The last sampling coincided in both cultivars with approximately 7-10 days before maturity.

Mean ribulose biphosphate carboxylase activities (Rubisco activities) for the 10 isolines showed a steady decrease in activity as maturity was approached. The sharpest decrease in activity took place in normal types, while the slowest decrease occurred in cytoplasmic green types. Genetic green types (d_1d_2) had slightly higher activities near maturity, and cytoplasmic greens were the highest at early stages. Genotypes d_1 and d_2 showed somewhat intermediate values in the last sampling date.

Only the genetic greens had a definite trend of continuously increasing mean specific leaf weights (SLWs) toward maturity in both cultivars. They had, in general, lower SLWs at early sampling dates, and the highest SLWs near maturity.

Total chlorophyll contents (Table 2) decreased linearly through sampling dates in all genotypes in both backgrounds, with the exception of d_1d_2, which first increased and then decreased to their lowest values. Normal types in both Clark and Harosoy had lower contents for all samplings, while types d_1 and d_2 had higher contents early and intermediate values late. Genetic greens had the highest values near maturity, whereas cytoplasmic green types were intermediate between normal and genetic greens, and slightly lower than d_1 and d_2 genotypes at all sampling dates.

Table 2. Total chlorophyll contents (mg/dm^2) of Clark and Harosoy isolines in soybeans (1981). (Means of 6 reps.)

		Sampling dates		
Background	Isoline	1st	2nd	3rd
Clark	Normal	5.2	4.6	3.6
	d_1	6.5**	6.2**	4.6
	d_2	7.4**	6.9**	4.4
	d_1d_2	7.1**	8.6**	6.3**
	cyt-G	6.7**	6.0**	4.2
Harosoy	Normal	7.6	6.1	3.3
	d_1	8.4	7.6**	5.1**
	d_2	8.0	7.6**	5.5**
	d_1d_2	7.9	8.2**	7.9**
	cyt-G	7.9	6.8	4.8**

*Significantly different from "normal" with P (0.05).

**Significantly different from "normal" with P (0.01).

Chlorophyll a contents followed essentially the same pattern as total chlorophyll, but with cytoplasmic greens being closer to normal types. The general trend for chlorophyll b through sampling dates in all lines of both cultivars was similar to that of total chlorophyll and chlorophyll a. Genetic and cytoplasmic greens, however, had the highest contents at the last two sampling dates, d_1 and d_2 genotypes were intermediate, and normal types had the lowest values.

For mean chlorophyll a:b ratios, the difference between cytoplasmic greens and the rest of the genotypes was readily apparent. The former had much lower ratios in both backgrounds, and the differences became more pronounced near maturity.

It is obvious from the results presented that, in chlorophyll-related traits, the green types behaved differently from normal types, and that there is a clearly distinct behavior between genetic and cytoplasmic greens. Also, there could have been some gene dosage effects, as suggested by the intermediate values of d_1 and d_2 types.

However, no analysis nor interpretation of the effects of d_1 and d_2 genes can be made because of the presence of *G* genes, unless we make the assumption that no physiological effects are associated with the *G/g* locus.

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1) ~~7~~ 45 Mutagenesis of soybeans.

The value of mutants in elucidating biochemical processes has been well-demonstrated in simple organisms. However, the approach has seldom been used in plants where simple selection schemes for biochemical characters can be difficult to devise. We have proposed that selection of a nitrate-reductase-(NR) deficient mutant of soybean could have a beneficial effect on nitrogen fixation. Recent isolation of induced NR mutants in barley (Kleinhofs et al., 1980) and pea (Feenstra and Jacobsen, 1980) indicated that a similar project might be successful in soybeans. However, reports on the comparison of various chemical and radiation mutagens in soybeans were scarce when we contemplated such a project. Rigorous comparison of different mutagens requires considerable experimental effort; variables affecting mutagenesis can include the mutagen, its concentration, treatment duration and pH, and presoak and postwash conditions. Evaluation requires large numbers in the M_1 and M_2 generations, and the experiment can rapidly become very unwieldy. However, for our objective of selecting the most effective mutagenic treatment from amongst several mutagens, a practical compromise was made, represented by the following approaches.

A preliminary experiment involved presoaking seed of 'Williams' for 16 hours in vigorously aerated water, changed after 2 and 5 h, then treatment with 50 and 100 mM ethylmethylsulfonate (EMS) (pH 7.0), 0.5 and 1.0 mM NaN_3 (pH 3.5), and 2.5 and 5.0 mM nitrosomethyl urea (NMU) (pH 5.5) for 3, 6, and 9 h. Treatments were carried out in a volume of 1 ml/seed, in 0.1 M phosphate buffer and with continuous aeration. After postwashing for 10 h in running tap water, 100 seed were immediately planted and emergence and frequencies of chlorophyll-deficient sectors were recorded after 21 days. Dose and treatment time with EMS affected emergence and sectoring in opposite directions, and the greatest yield of sectored M_1 plants/100 seed treated occurred with the 50 mM treatment for 9 h (Table 1). Most of the NMU treatments were too harsh, but the 2.5 mM treatment at 3 h produced the highest yield of sectors observed in the experiment. All the NaN_3 treatments were ineffective in producing sectoring. Based on the yield of sectored M_1 plants, the 9-h 50 mM EMS treatment and the 3-h 2.5 mM NMU treatment were selected for treatment of large quantities of seed, although the NMU treatment was arbitrarily increased to 5 h in an attempt to further increase the effectiveness.

The second experiment involved M_1 and M_2 comparison of the selected chemical treatments with gamma ray and unmoderated fission neutron irradiation treatments, each at two doses. The experiment was combined with treatment of large quantities of seed, so that M_2 seed of the most effective treatment would be immediately available. The chemical treatments were carried out in the same manner as in the preliminary experiment, except that practical limitations required that each mutagen treatment was split into two batches of 10,000 seed, which received 5-h and 9-h postwashes, respectively, instead of the original 10-h. Each radiation treatment dose involved

Table 1. Effect of various chemical mutagen treatments on M_1 soybean seedling characters in the greenhouse

Mutagen	Dose (mM)	Time (hours)	Emergence (%)	Plants with sectors[a] (%)
EMS	50	3	45	4
		6	45	4
		9	44	7
	100	3	34	5
		6	30	9
		9	25	11
NaN_3	0.5	3	42	0
		6	35	0
		9	32	0
	1.0	3	55	0
		6	47	0
		9	42	0
NMU	2.5	3	46	12
		6	44	b
		9	32	b
	5.0	3	32	b
		6	0	-
		9	0	-
Control[c]	---	9	84	0

[a]Sector defined as a chlorophyll-deficient region of the first trifoliolate apparently descended from one mutated cell.

[b]Plants very stunted, sectors not scored.

[c]Control was buffer treated (pH 7.0).

12,000 Williams and 8,000 non-nodulating 'Harosoy' seed. Eighty M_1 seed of each treatment were reserved for germination tests in the greenhouse, and the remaining seed were planted in the field in 1980. Frequencies of sectors were scored on 800 M_1 plants/treatment in the field, and frequencies of chlorophyll mutants on 600 M_2 seedlings/treatment were determined in the greenhouse.

The results confirmed that NMU was a more effective chemical mutagen than EMS under the experimental conditions used (Table 2). Shorter postwashing tended to decrease M_1 emergence, but increased M_1 sector and M_2 chlorophyll mutant frequencies, so that the yield of M_1 sectored plants/100 seed treated was greatest in the NMU 5-h postwash treatment. Gamma rays and fission neutrons also produced high yields of M_1 sectored plants;

Table 2. Effect of various chemical and radiation mutagen treatments on M_1 and M_2 soybean seedling characters

Mutagen treatment	Cultivar[a]	M_1 emergence	M_1 sectors[b]	M_2[c] chlorophyll mutants
		%	%	%
50 mM EMS				
9-h postwash	W	77	2.1 ± 0.59	1.0 ± 0.24
5-h postwash	W	75	2.6 ± 0.90	0.9 ± 0.56
2.5 mM NMU				
9-h postwash	W	62	3.4 ± 0.57	1.4 ± 0.86
5-h postwash	W	51	5.5 ± 0.60	3.1 ± 0.70
γ-rays				
20 kR	W	84	4.1 ± 0.65	0.6 ± 0.28
25 kR	W	74	4.8 ± 0.59	1.7 ± 0.65
20 kR	H	84	2.7 ± 0.54	0.4 ± 0.47
25 kR	H	72	5.0 ± 0.40	0.8 ± 0.39
fission neutrons				
1.7 kR	W	78	5.1 ± 0.47	1.4 ± 0.51
2.2 kR	W	95	3.5 ± 0.64	2.0 ± 0.51
1.7 kR	H	72	3.4 ± 0.28	0.8 ± 0.37
2.2 kR	H	79	3.8 ± 0.73	1.0 ± 0.41

[a]W = Williams; H = a non-nodulating isoline of Harosoy.

[b]Mean ± SD of eight randomly chosen 100-plant sections of row.

[c]Mean ± SD of six replicates of 100 plants/replicate.

emergence was less affected with radiation where seeds were treated dry, than with chemical treatment where seeds were partially germinated. The frequency of chlorophyll mutations in the M_2 was highest for the 5-h postwash NMU treatment. Correlation between frequencies of M_1 sectors and M_2 chlorophyll mutants was high within the chemical treatments ($r = +0.98$, $p < 0.05$), but less marked within the radiation treatments ($r = +0.33$, ns) or over all treatments combined ($r = +0.53$, $p < 0.10$). M_1 sectoring may, therefore, be most useful as an indicator of M_2 mutation rate when comparing treatments within mutagens, and may not be an accurate discriminator between mutagens. We selected the 5-h postwash NMU-treated M_2 seed to screen for NR mutants. No totally NR-deficient mutants have been isolated and reasons for this are discussed in the accompanying contribution. The M_2 plants did, however, display considerable visual variation, confirming an effective rate of mutagenesis with this treatment.

We have also done a preliminary experiment with some less commonly used mutagens where the objective was to establish suitable concentrations for soybeans and extensive data were not collected. Experimental conditions were as previously described, but with a 6-h treatment time and a 6-h post-wash. Details are given in Table 3. Only the hydrazine treatments caused complete germination failure, and the concentrations of all other mutagens fell within acceptable limits. Paper-towel germination is likely to under-estimate field emergence since we have observed considerable decreases in vigour in some mutagen treated material, but those data should provide a basis for anyone wanting to use these mutagens in soybeans.

Table 3. Effect of varying concentrations of seven chemical mutagens on germination of Williams soybeans

Mutagen[a]	Concentration range[b]	Germination[c]
	mM	%
Ethidium bromide	0.04 - 0.12	70 - 70
Hydrazine	100 - 200	0 - 0
L-ethionine	1.0 - 3.0	100 - 70
Maleic hydrazide	5 - 15	86 - 96
Nitrosoguanidine	0.1 - 0.5	38 - 65
Nitrofurantoin	0.002 - 0.2	83 - 62
Sodium azide	1 - 5	61 - 22

[a]All mutagens in phosphate buffer, pH 7.0, except nitrosoguanidine in acetate buffer, pH 5.5, and sodium azide in phosphate buffer, pH 3.0.

[b]Lowest and highest of three concentrations.

[c]Scored on 30 seed after 4 days in wet paper towels; figures represent germination in lowest and highest concentrations.

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2) Selection and inheritance of nitrate reductase mutants in soybeans.

Our primary objective in looking for nitrate reductase (NR) mutants in soybeans is to attempt to overcome the inhibition of nitrogen fixation by soil nitrate. The rationale depends upon blocking normal nitrate metabolism by finding defective NR mutants, thus liberating additional carbon and energy for use by nodules in nitrogen fixation. Additional benefits likely to result from the isolation of NR mutants in soybeans are a) a better understanding of normal nitrate metabolism and b) provision of easily selectable genetic markers.

Twelve thousand M_2 seedlings of 'Williams' were screened for chlorate resistance. Chlorate is reduced by NR to chlorite which produces characteristic toxicity symptoms; plants with normal NR show symptoms and plants with low or zero NR appear normal. The material screened had been treated with nitrosoguanidine, EMS, gamma rays, and EMS in four successive generations, and M_2 seed of the final mutagenesis was screened.

Three selections were verified as having low levels of NR activity when nitrate was present in the nutrient medium, and were designated LNR-2, LNR-3, and LNR-4. When grown in the presence of urea, these lines lacked the constitutive NR activity found in Williams grown under the same conditions (Table 1). Thus, NR activity in nitrate-grown Williams plants appears to be a summation of an inducible and a constitutive activity, and the mutant lines lack the constitutive component (Nelson et al., 1983).

Table 1. Leaf nitrate reductase activity of Williams, LNR-2, LNR-3 and LNR-4 grown on nitrate or urea

Nutrient N source	Williams	LNR-2	LNR-3	LNR-4
	$\mu mol\ NO_2^-\ (g\ fresh\ wt \cdot h)^{-1}$			
Nitrate	26.9 ± 3.9[a]	14.2 ± 3.5	11.1 ± 5.0	12.3 ± 2.8
Urea	16.0 ± 5.6	0.0	0.0	0.0

[a] *In vivo* +NO_3^- NR assay, mean ± SD for four replicates.

These lines also lack the ability to evolve $NO_{(x)}$ (NO and NO_2 collectively) from the *in vivo* NR assay, a characteristic of standard soybeans initially shown in 'Wells' (Harper, 1981) and subsequently verified in Williams and other soybean cultivars (Nelson et al., 1983 and unpublished). The biochemical basis of $NO_{(x)}$ evolution is not known, but since two reduction steps are necessary to take NO_3^- to NO_2^- to $NO_{(x)}$, the involvement of two enzymes is implicated. However, the concomitant disappearance of constitutive NR activity (NO_3^- to NO_2^-) and $NO_{(x)}$ evolution (NO_2^- to $NO_{(x)}$) in the selected mutants suggested a single gene mutation.

Segregation for constitutive NR activity in F_2 seedlings of crosses between Williams and each of the three selected lines indicated that absence of the character was inherited as a single recessive nuclear gene (Table 2). Of the combined total of 449 F_2 seedlings, 346 were also tested for $NO_{(x)}$ evolution and no recombinants were detected (where NR activity was absent, exogenous NO_2^- was supplied in the assay so that $NO_{(x)}$ evolution would not be substrate limited). Therefore, the joint absence of constitutive NR activity and $NO_{(x)}$ evolution appears to be due to mutation of a single gene. Inheritance of absence of both characters as a single recessive gene was confirmed in the F_3 of Williams x LNR-2 by analysis of 10 individuals in each of 16 lines; three lines were totally absent in both characters, four lines had both characters present in every plant, and nine lines were still segregating (χ^2_2 = 0.38, $0.80 < p < 0.90$ for a 1:2:1 expected ratio). Allelism tests, consisting of the evaluation of 10 F_2 seedlings from a single F_1 plant of each of the crosses, LNR-2 x LNR-3 and LNR-2 x LNR-4, showed no complementation for constitutive NR or $NO_{(x)}$ evolution, indicating that all mutations were at the same locus. LNR-2 is phenotypically indistinguishable from Williams, and, when grown on nitrate, accumulates reduced nitrogen at a similar rate (Ryan et al., 1983). Therefore, this NR mutation does not fulfill our initial objective. LNR-3 and LNR-4 are not impaired in their nitrogen metabolism, but they do accumulate dry weight at a slower rate than Williams. Since the NR lesion is at the same locus in all three lines, we conclude that LNR-3 and LNR-4 carry additional mutations unrelated to the expression of the NR gene. We propose naming the locus Nr_1 and hence the mutant will be nr_1. Seed of LNR-2 have been lodged in the Genetic Type Collection where it has been designated T276.

Table 2. Presence of constitutive NR activity and $NO_{(x)}$ evolution in F_2 seedlings of reciprocal crosses between Williams and LNR-2, LNR-3, and LNR-4

Cross	Number of F_2 seedlings		χ^2_1 (3:1)	P
	With NR and $NO_{(x)}$	Without NR and $NO_{(x)}$		
W[a] x LNR-2	54	21	0.36	0.50 - 0.70
LNR-2 x W	16	12	4.75	0.02 - 0.05
W x LNR-2	100	32	0.04	0.80 - 0.90
LNR-2 x W	31	9	0.13	0.70 - 0.80
W x LNR-3	42	6	4.00	0.02 - 0.05
LNR-3 x W	41	7	2.78	0.05 - 0.10
W x LNR-4	36	18	2.00	0.10 - 0.20
LNR-4 x W	19	5	0.22	0.50 - 0.70
Total	339	110	0.06	0.80 - 0.90

[a]This reciprocal set tested for presence of NR activity only.

Due to the staggered nature of the development of constitutive and inducible NR activity in soybean leaf tissue (Nelson et al., 1983), we would not expect chlorate to be successful in isolating an inducible NR mutant. Therefore, we have bulked and remutagenized LNR-2 and will screen for double NR mutants.

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3) Genes y_9 and y_{11} for similar chlorophyll deficiencies prove to be non-allelic

T219H and T135, two of the more vigorous chlorophyll-deficient types in the Genetic Type Collection, both have distinctly light green foliage throughout their life cycle. They are controlled by different genes since the T135 phenotype is caused by a homozygote, y_9y_9 (Probst, 1950), and the T219H phenotype by a heterozygote, $Y_{11}y_{11}$ ($y_{11}y_{11}$ has a bright orange-yellow seedling-lethal phenotype) (Weber and Weiss, 1959). However, because of the similar phenotypes, it has been suggested that y_9 and y_{11} may be multiple alleles at the same locus.

In crosses of normal soybeans x T219H, the F_1 population is 1/2 normal green and 1/2 vigorous light green like the male parent. The cross of L69-4755 (which is y_9y_9 from Clark 63^6 x T135) x T219H was made at Urbana, and the F_1 planted in the greenhouse in 1974-75. Of the 17 F_1 plants produced, 9 were normal green and 8 were weak plants with greenish yellow foliage distinctly weaker and more yellow than expected. They produced only 10 to 20 seeds each.

The F_2 was grown in the greenhouse in 1976-77. Results from F_1s of the same phenotype were similar and are combined in the table below:

		F_2				
		Green	Lt green	Gn-yellow	Yellow	χ^2 Prob.
F_1	Green $Y_9Y_9Y_{11}Y_{11}$	329	139			
	Expected (3:1):	351.0	117.0			.02
F_1	Gn-Yellow $Y_9y_9Y_{11}y_{11}$	20	27	37	25	
	Expected (3:3:6:4):	20.4	20.4	40.9	27.3	.44
	Genotype	Y_YY	$yyYY$	$YyYy$	$\_\ \_\ yy$	
			+ $YYYy$	+ $yyYy$		

This established that y_9 and y_{11} were not allelic, but we were interested in testing the unexpected phenotypic interactions further with larger populations.

The reciprocal cross T219H x L69-4755 was made in 1976 and the F_1 grown in the greenhouse at Ames. Of the 16 F_1 plants 8 were normal green and 8 were again weak yellowish green plants that produced from 0 (3 plants) to about 40 seeds.

The F_2 from these plants was grown in the greenhouse at Urbana in 1980-81, classified, and the F_2s were transplanted to the field and grown to maturity. The F_2 classification results are presented below:

		F_2				
		Green	Lt green	Gn-yellow	Yellow	χ^2 Prob.
F_1	Green $Y_9Y_9Y_{11}Y_{11}$	987	323			
	Expected (3:1):	982.5	327.5			.77
F_1	Gn-yellow $Y_9y_9Y_{11}y_{11}$	21	18	25	35	
	Expected (3:3:6:4):	18.6	18.6	37.1	24.8	.04
	Genotype:	Y_YY	$yyYY$	$YyYy$	$\_\ \_\ yy$	
			+ $YYYy$	+ $yyYy$		

The results here would better fit a 3:3:4:6 ratio (χ^2 P = 0.93) which would indicate that the $y_9y_9Y_{11}y_{11}$ genotype in this planting appeared similar to the lethal yellow seedlings, $\_\ \_y_{11}y_{11}$. We grew F_3 seedlings from all of the productive F_2 plants with the results given below. However, in the field, the greenish-yellow F_2 plants died at mid-season and so we have no confirmation of the $y_9y_9Y_{11}y_{11}$ phenotype.

F_2		F_3				
Genotype	No.	Green	Lt green	Gn-yellow	Yellow	χ^2 Prob.
$Y_9Y_9Y_{11}Y_{11}$	6	264				
(exp.):	(6.2)	(264)				1.00
$Y_9y_9Y_{11}Y_{11}$	15	492	147			
(exp.):	(12.4)	(479.3)	(159.7)			.24
$y_9y_9Y_{11}Y_{11}$	6		226			
(exp.):	(6.2)		(226)			1.00
$Y_9Y_9Y_{11}y_{11}$	12	118	257		148	
(exp.):	(12.4)	(130.8)	(261.5)		130.8	.17

Thus, the F_3 populations corroborated the F_2 results.

In this F_2 population the light green phenotype was distinguished into two classes and the darker light green plants all segregated in the F_3 and were therefore $Y_9Y_9Y_{11}y_{11}$. The lighter light green plants (with one exception, a stunted plant) proved to be $y_9y_9Y_{11}Y_{11}$. Thus, at least under some conditions, the T219H phenotype appears slightly darker than the T135 phenotype.

A summary of the phenotypes is given below:

Y_9 — Y_{11} Y_{11}	green
y_9 y_9 Y_{11} Y_{11}	light green
Y_9 Y_9 Y_{11} y_{11}	light green (darker than above)
Y_9 y_9 Y_{11} y_{11}	weak greenish yellow (lethal in field)
y_9 y_9 Y_{11} y_{11}	similar either to phenotype above (very slightly favored in data presented) or below, may prove to be intermediate.
— — y_{11} y_{11}	lethal orange-yellow seedling.

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1) 245 <u>Locating *wm* on linkage group 8</u>.

The genes reported on linkage group 8 (LG 8) are w_1, *wm*, and ms_1 (Soybean Genetics Committee, 1977). The recombination percentages between w_1 and ms_1 and w_1 and *wm* are 29.7 ± 1.6 and 2.2 ± 0.5, respectively. However, the order of the genes is not known. It may be w_1, *wm*, and ms_1, or *wm*, w_1, and ms_1. In order to determine the order of the genes, the chromosome number and constitution of F_2 progenies of hybrids between translocation 172-11-3 (purple flower, W_1 W_m) and T235 (magenta flower, W_1 *wm*) were determined.

The interchange chromosomes in 172-11-3 are recognizable in root tip squashes. The short interchange chromosome has the satellite; the other interchange chromosome is longer than any of the chromosomes of the standard complement. In hybrids involving 172-11-3, gametes with a duplication-deficiency, D(N2 T3 chromosomes), are functional in the female. Data of crosses between 172-11-3 (++) x T161 (w_1 +) and A77-139 (w_1 ms_1) have indicated that the w_1 locus is on the short interchange chromosome. Furthermore, data of a cross between 172-11-3 and A77-139 indicated that the breakpoint is between the locus of w_1 and ms_1 (Sadanaga, unpublished).

The *wm* locus can be at points shown in Figs. 1a, 1b, or 1c. Data in Table 1 rule out the possibility that the correct order is that shown in Fig. 1a because all N/D (N2 N4/N2 T3) progenies had magenta flowers. If the correct order is that shown in Fig. 1b, N/N (N2 N4/N2 N4) chromosome-plants with purple flowers would be expected to occur at a recombination frequency about 4%, the sum of the recombination frequencies between w_1 and the breakpoint 2% (Sadanaga and Grindeland, submitted for publication) and w_1 and *wm* 2.2%. No crossovers were detected in 90 N/N and 19 N/D plants (Table 1). The order shown in Fig. 1c, w_1, *wm*, breakpoint, and ms_1, fit the data in Table 1.

Table 1. Chromosome number and constitution, and phenotype of F_2 soybean progenies of a cross between T235 (magenta) x 172-11-3 (purple)

Chromosome		Flower color		
Number	Constitution	Purple	Magenta	Total
40	N/N	0	90	90
	N/T	136	0	136
	T/T	53	0	53
	N/D	0	19	19
	T/D	12	0	12
Total		201	109	310

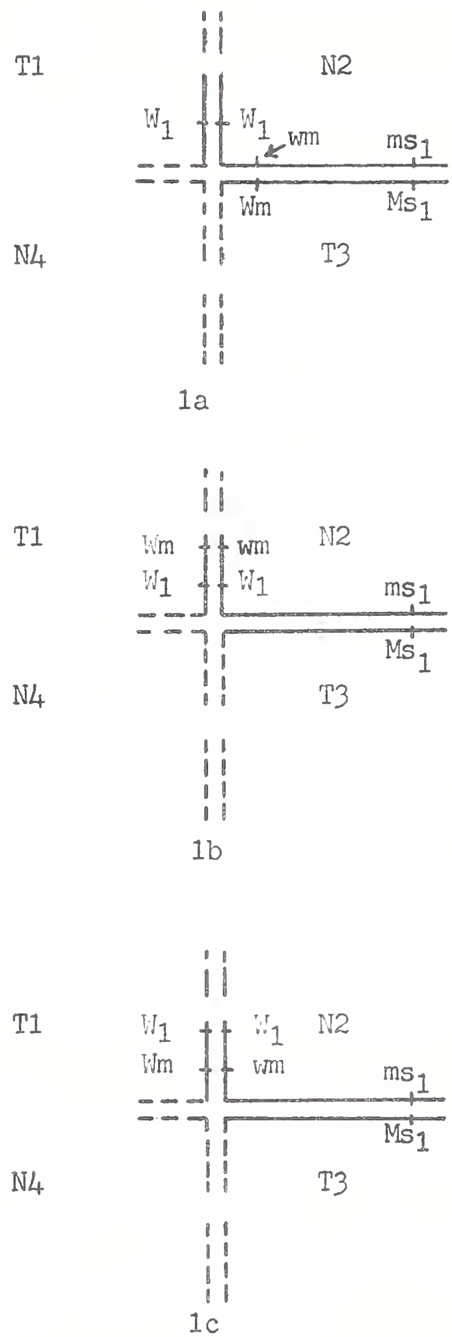

Figure 1. Diagrams showing three possible order of genes

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2) 45 Four additional lines showing nonfluorescent roots.

Fluorescence in soybean roots was first described by Chmelar (1934) and by Chmelar and Mostovoj (1934). Reports of nonfluorescing root phenotypes in both *Glycine max* and *G. soja* have been made by Grabe (1957), Fehr and Giese (1971) and Broich (1978). Genetics studies by Delannay and Palmer (1982) indicate that absence of root fluorescence in *G. max* is controlled by four independent genes; three of these genes are recessive (fr_1, fr_2 and fr_4) and one is dominant (Fr_3). To date, the geographic distribution of these four genes appeared to be unequal; fr_1 was found in accessions from the Far East and Europe; fr_2 was found only in European accessions, while Fr_3 and fr_4 were found only in accessions from Asia.

Herein, we report the genetics of four additional lines which have nonfluorescing root phenotypes. The lines are described in Table 1; the results of genetic studies are reported in Table 2.

The Chinese cultivar 'Mandell' carries the nonfluorescent allele fr_2. Mandell was a selection from the cultivar 'Manchu' made at the Indiana Agricultural Experiment Station and represents the first non-European accession found to carry fr_2.

PI 372418 is the fifth Yugoslavian accession found to carry fr_1. A82g-27, a recent introduction from the People's Republic of China, is the third accession from China known to carry fr_1. A82g-27 phenotypically resembles our standard fr_1 line 'Minsoy'.

PI 339871B is the second nonfluorescent accession of *G. soja* to be classified genetically. It was originally collected on Cheju Island off the southern coast of the Korean peninsula. PI 339871 was morphologically heterogeneous and was separated into "A" and "B" forms by germplasm curators in the United States. Broich (1978) reported the presence of root fluorescence in the "A" form and both presence and absence of root fluorescence in the "B" form. Data presented here indicate that nonfluorescence in PI 339871B is due to fr_4, an allele previously known only from accessions of *G. max*.

Of the 116 Korean accessions of *G. max* tested so far (Broich, 1978; Delannay and Palmer, 1982; Palmer and Yost, unpublished), only PI 424078 has nonfluorescent roots. PI 424078 entered the United States in a large collection of *G. soja* lines and was later classified as *G. max* by R. L. Bernard because of its morphological similarity to the domesticated species. Nonfluorescence in PI 424078 is controlled by Fr_3, an allele found also in PI 65549, an accession of *G. soja* from Heilungkiang Province, People's Republic of China.

Thus, from Korea we have discovered one accession of *G. soja* with an allele previously found only in *G. max* (PI 339871B carrying fr_4) and one accession of *G. max* that is phenotypically somewhat similar to *G. soja* (Delannay and Palmer, 1982) and carries an allele for nonfluorescent roots (Fr_3) known only from an accession of *G. soja*. These data seem to corroborate the numerous reports of introgression between *G. max* and *G. soja* (see Broich, 1978). Additional genetic studies of root nonfluorescence in *G. max* and *G. soja* accessions from Korea are now in progress with the hope of further elucidating evolutionary processes within the Genus *Glycine* subgenus *Soja*.

Table 1. Soybean accessions showing nonfluorescent roots when exposed to ultraviolet light

Accession	Country of origin
Mandell	The People's Republic of China (Northeast; selection from the cultivar Manchu)
PI 339871B*	Korea (Cheju Island)
PI 372418	Yugoslavia
A82g-27+	The People's Republic of China (Teiling District)

**Glycine soja*; all others are *Glycine max*.

+Plant introduction number not yet assigned.

Table 2. Root fluorescence of F_2 progenies from crosses between nonfluorescent soybean accessions and a fluorescent standard line and the four standard nonfluorescent lines, respectively

Unknown	Fluorescent	Standard nonfluorescent lines			
		fr_1 Minsoy	fr_2 PI 290136	Fr_3 PI 424078	fr_4 PI 404154
	F* : NF+	F NF	F NF	F NF	F NF
Mandell	245 : 80	123:96	0:238		35 : 30
PI 339871B	42 : 15	43:85	161:112		0 :100
PI 372418	135 : 55	0:40			
A82g-27	117 : 38	0:54			

*F = fluorescent roots.

+NF = nonfluorescent roots.

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3) 145 Fr_1 and fr_1 near-isogenic lines [1-2]

The substances responsible for fluorescence in soybeans roots have not been identified and their function is not known, but the trait is useful in both physiological and genetic research. Therefore, we decided to develop near-isogenic lines in the cultivar 'Hark' with the Fr_1 Fr_1 (root fluorescent) genotype and the fr_1 fr_1 (root nonfluorescent) genotypes.

The original cross was 'Minsoy' fr_1 fr_1 x Hark Fr_1 Fr_1. A nonfluorescent F_2 plant was selected and used as male parent with Hark as female. The following crossing schedule was employed:

F_1 Minsoy x Hark

F_2 selected fr_1 fr_1 plant

BC_1 Hark x fr_1 fr_1

BC_2 Hark x BC_1F_1

BC_3 Hark x Fr_1 Fr_1

x Fr_1 fr_1

Starting at BC_3, we used eight different plants of BC_2F_1 in crosses with Hark. We made eight or more hybrid seeds from each of the eight BC_2F_1 plants. We checked root fluorescence of selfed seed from each of the eight plants. BC_3F_1 seed from one cross between Hark and a BC_2F_1 plant segregating for root fluorescence were saved to use as a parent for the next generation.

BC_4 as described for BC_3

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BC_6 We selected one plant that was $Fr_1\ fr_1$, based on progeny testing. F_2 plants that were Fr_1__ and $fr_1\ fr_1$ were selected. F_2-plant progeny rows from the fluorescent types $Fr_1\ Fr_1$ and $Fr_1\ fr_1$ were planted and genotypes identified, based on nonsegregation and segregation for fluorescence.

About 100 seed of the genotypes $Fr_1\ Fr_1$ and $fr_1\ fr_1$ were planted in the field in 1982. Plants of each genotype were single-plant threshed and progeny tested to confirm their genotypes. No misclassifications were evident. Seed of each genotype were bulked separately. Seed of these near-isogenic lines are available for distribution.

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4) Trisomic inheritance of a chimera in soybean.

Introduction: In the summer of 1978, four chlorophyll-chimeric plants were observed within a population of 'Clark'. The four plants had a similar phenotype, and were surmised to originate from a common parent. These four plants were single-plant threshed. Progeny rows from these plants were grown the summer of 1979 to look for segregation; progeny rows might include yellow plants and green plants, in addition to chimeric progeny. No segregation was observed; progeny were all chimeras, with no yellow or green segregants.

Reciprocal crosses with green plants were made to examine the inheritance of the trait. Also, some crosses were made to provide a preliminary examination for linkage relationships, in case the trait proved to be controlled by genetic rather than cytoplasmic inheritance.

Examination of F_1 plants suggested genetic rather than cytoplasmic inheritance, as reciprocal F_1s were green. Determination of the inheritance of the character was inconclusive upon examination of the F_2 populations; however, it was determined that a gene controlling the character might be located on the extra chromosome of trisomic line Tri A (see Palmer, 1976).

Subsequently, this study was initiated to identify: 1) the mode of inheritance of the trait, and 2) whether a gene or genes controlling the trait are located on the extra chromosome of Tri A.

Materials and methods: Mutant plants were crossed to Trisomic A plants, and the F_1 plants grown in the summer of 1981. Attempts to obtain chromosome counts on F_1 plants were unsuccessful. F_2 progenies were germinated in the sandbench the following winter, and were classified as green or chimeric, at the first trifoliolate stage.

Chromosome counts were obtained on F_2 plants from each F_2 family to determine the chromosome number of the F_1, using the method of Palmer and Heer (1973). F_3 progenies were developed from F_2 plants that had elevated ratios of green-to-chimeric plants, by transplanting these F_2 plants to the field in the summer of 1982. F_2 plants were single-plant threshed, and resulting F_3 progenies were classified by observing phenotypes of plants grown in the sandbench the following winter.

Results and discussion: Segregation ratios of F_2 progenies formed two distinct groups (Table 1). One group exhibited a green:mutant segregation ratio of between 3.0:1 and 4.3:1. The second group exhibited a substantially higher proportion of green plants, with segregation ratios ranging from 12.4:1 to 22.0:1. Percentage emergence was very high, and did not appear to be an influencing factor.

It was suspected that the F_2 progenies exhibiting an elevated frequency of green plants resulted from trisomic F_1 plants. By checking chromosome numbers of F_2 plants from each progeny, the suspicion was confirmed (Table 2). Variable numbers of individuals in each class are due to variable percentage germination.

Each of the F_2 progenies with higher ratios of green to chimeric plants was found to contain plants with 41 chromosomes; it can be safely concluded that these progenies were derived from trisomic F_1 plants. None of the plants from progenies with segregation ratios of 3.0-4.3:1 was found to be trisomic. It is assumed that these progenies were derived from F_1 plants with 40 chromosomes.

Verification for trisomic inheritance was obtained by examining the segregation of the F_3 progenies (Table 3). Progenies from 40-chromosome plants that segregated for the trait exhibited a 3.4:1 ratio. Progenies from 41-chromosome plants that segregated exhibited a 12.5:1 ratio.

These data, summarized in Tables 1, 2, and 3, provide the information necessary for establishing trisomic inheritance of the mutant trait. The duplex condition in trisomic heterozygotes (AAa) results in a greatly reduced frequency of homozygous recessive individuals. The chi-square fit of the segregation of progenies from trisomic plants to segregation of progenies from disomic plants (Tables 1 and 3) indicates a difference at the 1% level of probability. This provides sufficient proof that a locus controlling the trait is located on the extra chromosome of the line Tri A.

Segregation ratios from 40-chromosome plants provide a way to examine the inheritance of the mutant trait. In 1981, the segregation of F_2 progenies was about 3.7:1, pooled over all progenies (Table 1). Many of the classes did not fit a 3:1 ratio; likewise, the pooled information did not fit a 3:1 ratio. The data were observed to be homogeneous. In 1982, the segregation ratio from 40-chromosome F_3 progenies was about 3.4:1, pooled over all segregating progenies (Table 3), and was homogeneous as well. The data from these two sources are homogeneous with respect to each other; the ratio using these data combined is 3.7:1.

Table 1. Observed segregation of green and chimeric soybean plants in F_2 progenies. Progeny groupings are according to a) those exhibiting a lower frequency of green plants, and b) those exhibiting a higher frequency of green plants

F_2 progeny number	No. of green plants	No. of chimeric plants	Total	% emergence	Observed ratio:1	χ^2 fit to 3.7:1	χ^2 fit to 3.0:1
a)							
154	490	137	627	96.5	3.6	0.10	3.32
155	723	170	893	99.2	4.3	2.82	16.94**
157	539	143	682	97.4	3.8	0.06	5.91*
158	832	196	1028	97.9	4.2	3.17	19.30**
160	331	106	437	97.1	3.1	2.21	0.13
161	675	185	860	95.6	3.6	0.01	5.58*
164	710	195	905	95.3	3.6	0.02	5.76*
166	596	186	782	97.8	3.2	2.78	0.62
167	563	149	712	94.9	3.8	0.07	6.30*
168	162	54	216	86.4	3.0	1.72	0.00
169	269	86	355	88.8	3.1	1.76	0.11
171	267	75	342	97.7	3.6	0.07	1.72
172	481	119	600	100.0	4.0	0.81	8.54*
Totals	6638	1801	8439	96.4	3.7	15.60	74.23**
Pooled χ^2						0.00	60.25**
Homogeneity χ^2 12 df						15.60	13.97
b)							
156	700	32	732	97.6	21.9	125.57**	
159	747	34	781	91.9	22.0	134.27**	
162	520	42	562	93.7	12.4	64.39**	
163	481	26	507	92.2	18.5	79.37**	
170	549	29	578	88.9	18.9	91.75**	
Totals	2997	163	3160	92.9	18.4	495.35**	
Pooled χ^2						493.00	
Homogeneity χ^2 4 df						2.35	

*Significant at the 5% level of probability.

**Significant at the 1% level of probability.

Table 2. Chromosome counts made on remnant soybean seed of F_2 progenies evaluated for segregation. Progenies are grouped according to segregation ratios as in Table 1

F_2 progeny number	No. with 40 chrom.	No. with 41 chrom.	No. with 42 chrom.	No. of chimeric plants
a)				
154	12			--[a]
155	10			--
157	10			--
158	10			--
160	10			--
161	10			--
164	4			--
166	9			--
167	10			--
168	12			--
169	13			--
171	9			--
172	11			
Totals	130			
b)				
156	15	4		
159	7	6	1	2
162	9	9		2
163	4	12	1	1
170	14	6		1
Totals	49	37	2	6

[a]Plants were discarded before classification was done.

Table 3. Observed segregation of green and chimeric soybean plants in F_3 progenies. Progeny groupings are according to a) those derived from 40-chromosome F_2 plants, and b) those derived from 41-chromosome F_2 plants

F_2 progeny number	F_3 progeny number	No. of green plants	No. of chimeric plants	Total	% emergence	Observed ratio:1	χ^2 fit to 3.4:1	χ^2 fit to 3:1
a)								
156	355	130	42	172	86.0	3.1	0.25	0.03
	347	149	45	194	97.0	3.3	0.02	0.34
159	386	133	42	175	87.5	3.2	0.14	0.09
162	388	154	38	192	96.0	4.1	0.99	2.78
163	420	144	40	184	92.0	3.6	0.12	1.04
170	511	143	45	188	94.0	3.2	0.14	0.11
Totals		853	252	1105	92.1	3.4	1.66	4.39
Pooled χ^2							0.00	2.84
Homogeneity χ^2 5 df							1.66	1.55
b)								
156	349	57	3	60	60.0	19.0	10.81**	
163	415	180	12	192	96.0	15.0	29.89**	
	423	141	15	156	78.0	9.4	15.42**	
	418	173	15	188	94.0	11.5	23.48**	
170	521	173	13	186	93.0	13.3	26.43**	
Totals		724	58	782	86.9	12.5	106.03	
Pooled χ^2							105.19**	
Homogeneity χ^2 4 df							0.84	

These segregation data do not fit either a 3:1 segregation, or a 13:3 segregation pattern, when a chi-square goodness-of-fit test is used. One possible reason that a 3:1 segregation does not fit could be reduced emergence of seedlings homozygous for the mutant trait. However, emergence levels were quite high, especially for the F_2 data, and do not appear to be the cause of a poor fit. Another reason could be reduced gamete or zygote viability associated with the mutant trait. Such phenomena have been observed to skew segregation for other mutant traits. If a 13:3 ratio due to digenic inheritance was expected, it should be possible to find chimeric plants in an F_2 progeny segregating green plants the following generation. These have not been observed to date; however, only six chimeric F_2 plants have been progeny tested. Additional chimeras will be identified in 1983 and single-plant threshed. These chimeras will be progeny tested. Linkage between two loci could explain the deviation from the expected segregation of 13:3.

With the data presently available, the inclination is to accept the simpler hypothesis of a reduced transmission rate of the mutant causing the deviation from the expected 3:1 ratio. No gene symbol or Genetic Type Collection number is being requested at this time.

Summary: Though primary trisomics in soybeans have been available for use in gene mapping studies for several years (Palmer, 1976; Sadanaga and Grindeland, 1979), no reports exist in the literature of linkage groups or loci being located on chromosomes through observation of trisomic inheritance. Soybeans have 40 chromosomes, small and for the most part morphologically indistinguishable. Primary trisomics will almost certainly need to be utilized to establish the 20 linkage groups of soybeans and to associate each with a particular chromosome. And, in turn, it is necessary to associate a linkage group or locus with a chromosome in order to distinguish the different primary trisomics. Each new mutant trait available and each new linkage relationship identified will help to establish the basic genetic information necessary for efficient soybean cytogenetic study.

This study of trisomic inheritance of a mutant trait is an example of the type of genetic studies that will be required to map the chromosomes of the soybean genome. Tri A is not associated with any of the linkage groups presently known in soybeans. Therefore, in one sense, this study defines a new linkage group. Also, an additional mutant for use in future cytogenetic studies is identified.

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1) 145 Insect population dynamics in relation to soybean narrow and broad leaf isolines [ ].

A broad spectrum of stimuli can be an important factor influencing insect orientation, feeding and oviposition on most plants. Behavioral responses to visual and chemical stimuli are important factors in host selection. Color and form of plants and plant parts are among these stimuli (Saxena, 1975). Within commercial soybean varieties, leaf form varies in width and, therefore, is a factor which could influence insect orientation and ultimate population establishment.

A study was initiated in 1980 to evaluate the response of insect populations to soybeans of narrow and broad leaf types. Knowledge of significant differences in the establishment of pest populations on either growth type could be beneficial due to the simple nature of inheritance of the phenomenon and its ease of incorporation into planting practices.

Throughout the growing season, 13 major insect species were monitored on two isoline pairs, V75-776 (narrow), V75-778 (broad), V75-811 (narrow), V75-814 (broad), (obtained from Dr. Glenn Buss, Virginia Polytechnic Institute). Populations of beneficial species as well as those of most pest species were uniform among growth types. However, a difference in responses between lines and between leaf types may have occurred for two pest species. Although differences were significant only at the 10% level, green cloverworm populations were greater in all years on the narrow leaf type V75-811 than on the broad leaf type V75-814. Potato leafhopper populations responded similarly on the second isoline pair V75-776 and V75-778. It is noteworthy that the two insect species responded similarly to the narrow leaf type of different isolines.

Elicited stimuli are specific to each plant species as are perceived stimuli to each insect species. In association with the isolines included in the study and with narrow leaf commercial varieties, environmental factors and plant-elicited stimuli other than leaf type could serve to enhance or mask a response to leaf type such that population differences could be important.

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2) Tactics for management of soybean pest complexes: Potential of entomopathogens and commercial microbial insecticides for suppression of the silver-spotted skipper soybean pest

The silver-spotted skipper (*Epargyreus clarus*), having become increasingly more destructive to Maryland Eastern Shore soybeans, is being studied as a candidate for biocontrol. Nordin (1975) described a possible viral pathogen isolated from a decayed skipper. Without a clear knowledge of the micro-flora population of a live insect it is difficult to conclude, from the presence of a microorganism on a dead insect, that a pathogen exists, since numerous species of bacteria multiply rapidly in dead insects. Thus, in this preliminary study, skippers were examined before they were moribund or dead.

Laboratory rearing of the silver-spotted skipper was unsuccessful. In late July, 1982, through September, 10 collections (different periods) of young larvae were made and reared each time in batches of 25 on soybean leaves in quart size paper cans at 86-88°F. After three days, five larvae from each container were randomly picked and prepared for examination. Preparation consisted of ligaturing each insect at the anterior and posterior orifices to prevent entrance of surface sterilizing agents into the hemocoel; dipping into 70% ETOH (2 sec), sodium hypochlorite (4 min), 10% sodium thiosulphate (4 min), and then three changes of sterile distilled water. After placing the insect in a sterile dissecting dish a cut was made along the dorsal line to enable a capillary tube to be inserted into the hemocoel to withdraw blood and body fluids. The blood and fluids were diluted in 2 ml sterile water and plated onto nutrient agar. The resulting bacterial colonies were selected, subcultured and the isolated organisms were identified by the following: Gram, spore, capsule and flagella stains; production of acetoin and acetylmethylcarbinol, hydrolysis of starch, gelatin, protein, and lipids; nitrate reduction; indole, urease, oxidase and catalase production; citrate utilization, phenylalanine deaminase and production of arginine, ornithine and lysine decarboxylase, and metabolism of carbohydrates: glucose, lactose, sucrose, xylose, maltose and arabinose. Seventy-seven isolates were made and, on comparison of characteristics, these were found to comprise replicates of several different strains.

The following isolates were obtained from the hemocoels of the silver-spotted skippers: achromogenic *Serratia marcescens*, *Pseudomonas aeruginosa* and *P. putida*, *Enterobacter aerogenes* and *E. cloacae*, *Micrococcus luteus*, *Citrobacter freundi*, *Alcaligenes faecalis*, *Flavobacterium* sp., and *Bacillus cereus*.

Although some of these organisms are known to be associated with insects, they are not necessarily considered pathogenic (e.g., *Alcaligenes* and *Flavobacterium*). Therefore, experimental tests on pathogenicity are required. Larvae from which *Bacillus cereus* were obtained did not appear sick. Strains of *Bacillus cereus* would appear to be the best candidate for biocontrol because of its spore-forming ability. The insecticidal organism *Bacillus thuringiensis* is an entomogenous strain of *B. cereus*. However, some strains vary in their abilities to produce lecithinase and phospholipase which render them more powerful as pathogens.

The silver-spotted skipper is presently in hibernation. Corn earworms will, therefore, be used to test the pathogenicity of some of the isolates, primarily the lipolytic and proteolytic isolates and the *Bacillus cerëus* strain in particular, using only feeding tests. Those organisms found to be pathogenic to corn earworms will be tested against the skipper this spring as well as commercial insecticides.

Reference

Nordin, G. L. 1975. A nuclear polyhedrosis virus from the silver-spotted skipper, *Epargyreus clarus* (Lepidoptera: Hesperiidae). J. Invertebr. Pathol. 16:131-132.

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3) 245 Harvest index of selected soybean germplasm [ ].

The distribution of total dry matter accumulation or biological yield in crop plants is very important in achieving high crop yields. In crop plants where the seed portion constitutes the product of economic or agricultural yield it is desirable that a greater proportion of available energy will be utilized for seed than nonseed production. The proportion of biological yield represented by economic yield was defined as harvest index (HI) by Donald (1962) and as seed yield efficiency (S.Y.E.) by Joshi and Smith (1976).

There is evidence that improvement in yield of crops has resulted in part from unconscious selection for high HI, especially where the reproductive parts constitute economic yield. Van Dobben (1962) demonstrated that, in 50 years of wheat breeding, the grain:straw ratio increased from 0.51 to 0.66 representing 29% increase in yield. Similar changes have been observed in barley (Thorne, 1958; Watson et al., 1958, and 1963), rice and peas (Donald, 1962), corn (Stinson and Moss, 1960; Sowell et al., 1961) and drybeans (Wallace and Munger, 1966). It is likely that, among the 10,000 soybean plant introductions in the germplasm collection maintained by the USDA, sufficiently high variability in HI exists. PIs with high HI may be utilized to increase the seed yielding ability of the present commercial soybean cultivars if they can be identified in a screening test. This report represents efforts at the University of Maryland Eastern Shore Soybean Research Institute to evaluate the HI of several soybean plant introductions within the RR3 project.

Seed of soybean plant introductions belonging to maturity groups III to VI, obtained from the USDA germplasm collection at Urbana, Illinois and Stoneville, Mississippi, were used in experiments at the University of Maryland Eastern Shore experimental farm. A number of PIs in MG III, IV and V were tested in the field in 1982. The field tests consisted of three-row plots in three replications for each PI entry. A plot measured 6 m x 0.5 m and entries were randomized in each replication. At physiological maturity, four plants were harvested from the center row of each plot, oven dried at 70°C for 24 h and the seeds and straw weighed separately. HI was calculated as seed dry matter and nondry matter.

Table 1 represents a ranking of HI of MG IV material. HI ranged between 0.41 and 1.68. About 50% of the entries in MG IV had HI equal to or greater than 1.00. Several of the PIs were found in the group that had high HI.

Almost all the entries matured at the same date. Yield data are being analyzed for statistical differences and correlations. However, trends seem to suggest positive correlations that may be exploited in improving the yield of commercial soybeans with some of the PIs which so far have not been utilized.

Table 1. Ranking of harvest index (HI) in soybean cultivars and plant introductions (PI) in Maturity Group IV

Cultivar or PI no.	HI	Cultivar or PI no.	HI	Cultivar or PI no.	HI
Hurrelbrink	1.68	83.944	1.16	82.509	1.01
80.828-2	1.66	86.007	1.16	Virginia	1.00
82.295	1.56	Patterson	1.15	82.534	1.00
81.042-2	1.51	Bethel	1.14	83.925	1.00
70.013	1.50	FC31.630	1.14	FC31.685	0.99
Lawrence	1.48	62.202-2	1.14	19.976-2	0.99
Clark 63	1.46	62.248	1.14	80.479	0.99
85.658	1.45	86.060	1.14	83.853	0.99
80.834-1	1.42	19.979-4	1.13	85.505	0.99
80.498-1	1.41	83.891	1.12	85.619	0.99
81.764	1.41	85.663	1.12	Ebony	0.98
Cutler	1.40	Chief	1.11	Perry	0.98
70.467	1.39	Emerald	1.09	68.449	0.98
80.837	1.39	Kaikoo	1.09	82.259	0.98
84.679	1.37	Patoka	1.09	85.506	0.98
Douglas	1.35	Wilson 6	1.09	82.263-1	0.97
85.590	1.35	FC31.946	1.09	19.979-1	0.95
Imperial	1.34	54.606-2	1.08	60.269-2	0.95
Jefferson	1.33	82.218	1.08	85.519	0.95
80.828-1	1.33	82-264	1.08	Higan	0.94
82.296	1.33	Crawford	1.07	54.615-2	0.94
85.624	1.32	Kahala	1.07	82.555	0.94
Desoto	1.31	70.208	1.07	83.858	0.94
Oksoy	1.31	82.527	1.07	Kailua	0.93
84.669N	1.31	85.420	1.07	82.326	0.93
83.889	1.30	Shiro	1.05	84.594	0.93
Green & Black	1.29	64.747	1.05	85.550	0.93
84.944	1.29	79.870-4	1.05	Aoda	0.92
Franklin	1.28	80.777	1.05	82.307	0.92
80.847-2	1.27	84.985	1.05	83.923	0.92
Pixie	1.26	Kent	1.04	84.912	0.92
82.291	1.26	19.979-3	1.04	AK(FC30.761)	0.91
84.939	1.25	70.825-1	1.04	84.724	0.91
54.617	1.17	82.210	1.04	Emperor	0.90
80.834-2	1.17	54.600	1.03	FC31.557	0.90
81.037-5	1.17	54.610-4	1.03	80.030	0.89
83.945-4	1.17	54.606-1	1.02	83.893	0.89

Table 1. *Continued*

Cultivar or PI no.	HI	Cultivar or PI no.	HI	Cultivar or PI no.	HI
84.713	1.17	Cutler 71	1.01	84.807	0.89
84.959	1.17	Sango	1.01	85.469	0.89
Miles	1.16	82.312N	1.01	86.112-1	0.89
19.979-4	0.89	Hokkaido	0.81	86.103	0.74
Kingston	0.88	Wilson	0.81	55.887	0.73
62.199	0.88	84.639	0.81	61.944	0.72
63.945	0.88	AK(Kansas)	0.80	56.563	0.71
70.490	0.88	80.488	0.80	58.955	0.71
80.034-1	0.88	81.037-1	0.80	Wilson 5B	0.67
Wabash	0.87	86.062	0.80	80.473	0.66
Custer	0.85	Morse	0.79	83.881A	0.66
Hahto/Michigan	0.85	84.908-1	0.79	60.970	0.65
84.960	0.85	19.979-6	0.78	Peking	0.64
68.011	0.84	83.946	0.77	54.608-4	0.63
85.424	0.84	19.979-7	0.76	Sooty	0.62
Gibson	0.83	64.698	0.76	82.558	0.61
61.947	0.83	84.660	0.76	86.109B	0.61
82.325	0.83	FC03.546	0.75	83.915	0.53
83.892	0.83	Wilson 5	0.74	63.468	0.41
86.134-1	0.83	84.664	0.74		

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1) Estimates of variation and heritability for nodule mass and recovery of *Rhizobium japonicum* strain 110.

Introduction: The increase of biological dinitrogen fixation has been an illusive and rather stochastic area of research for many soybean workers. One aspect of the symbiosis that merits more attention is the identification of genetic variability in host plants for the traits associated with fixation and the utilization of this variability in plant breeding programs. The purpose of the present study was to provide information on genetic variability for nodule mass and recovery of strain 110 in three soybean populations.

Materials and methods: The parents used to generate the three populations used in this study were plant introductions identified by Kvien et al. (1981) as showing diversity in their ability to form nodules with the indigenous *R. japonicum* strains (primarily serogroup 123). A rating system was set up on a scale of 1-6, 1 = low nodule mass to 6 = high nodule mass (mass, meaning visual estimates of nodule number and nodule size). PI 372415B and PI 68622 were given a rating of 6. PI 91119 and PI 189922 were classified as 1 and 2, respectively, for their amount of nodule mass. The cross PI 372415B x PI 91119 was made and 20 F_3-derived F_5 and F_6 lines from it constitute population 1. Population 2 was made up of 46 F_3-derived F_5 and F_6 lines from the cross PI 372415B x PI 189922. Population 3 contained 31 F_3-derived F_5 and F_6 lines from the cross PI 372415B x PI 68622. The 97 lines, the four parents and seven adapted varieties were planted in 1982 at Rosemount, St. Paul and Becker, MN. The experimental design consisted of four replications of a split-plot strip design. A peat-base inoculant containing *R. japonicum* strain 110 (an effective N_2-fixer) was applied with the seed at planting in one row of the two-row plot. Root cores were taken from each row in late July and ratings given according to the aforementioned scale. Sixteen nodules were taken at random from the sampled root systems and serotyped by the quick-test agglutination method (Damirgi et al., 1967) to identify the strain(s) of rhizobium forming each nodule.

Results and discussion: Previous researchers (Lawson, 1980; Gupta et al., 1982) subdivided a line's nodulation response into several components (i.e., nodules/plant and dry or fresh nodule weight/plant). Estimates of variances and heritabilities for these components differed between the two studies. In an attempt to further explore the potential sources of variability involved, three dissimilar populations and three diverse locations were used in the present study.

Estimates of means, ranges, variances and heritabilities for nodule mass for the three populations and three locations are presented in Table 1. Nodule mass/plant was significantly different among populations at Becker and St. Paul. The three locations were significantly different for nodule mass/plant. The means across populations were 1.89, 1.99 and 2.90 for St. Paul, Rosemount and Becker, respectively. Population 1 consistently had the highest nodule mass rating across all locations. The range in ratings

was largest at Becker. The heritability estimates on an entry-mean basis were consistent for each population across locations except in one instance. Estimates of heritability across locations based on entry-means were 40.73%, 67.94%, 57.67% for population 1, population 2 and population 3, respectively. Progress from selection for nodule mass should be possible if selection is based on replicated plots across locations. Use of the visual rating system for nodule mass as previously described in this paper showed a good correlation to the ranking of genotypes based on actual measurements of nodules/plant and fresh nodule weight. The use of this visual rating system would allow a much larger sample to be evaluated for nodulation ability and allow this evaluation to be done in the field. The inclusion of visual nodule mass as a selection criterion hinges on the relationship of nodule mass to yield. Some yield responses were noted in this study but the data are still being analyzed.

Previous research on the recovery of introduced rhizobium from soils containing large naturalized populations also show some divergence in conclusions. Kvien et al. (1981), in screening 85 diverse genotypes, found some genotypes that preferentially formed a significant percentage of their nodules with strain 110; however, a large amount of variability was present for recovery of strain 110 due to environmental effects. Kvien reported recoveries of inoculant strains as high as 40.0-50.0%. Lawson (1980) found location means for recovery of strain 110 in the range of 8.0% to 21.0%. Lawson reported a heritability estimate of 30.5% for the recovery of strain 110 across three locations. Ellis (1982) found inoculation with high rates of *Rhizobium japonicum* did not significantly increase the recovery of strain 110 in soybean nodules.

Table 2 contains estimates of means, ranges, variances and heritabilities for the recovery of strain 110. The three locations were significantly different for percent 110 recovered. Means averaged over the three populations were: 9.04%, 9.14% and 11.48% for Becker, Rosemount and St. Paul, respectively. Population 2 had the highest recoveries of strain 110 at all three locations. The widest range for recovery was 0.00% to 31.00%, which occurred at Becker. Large environmental variances were observed for recovery of strain 110 for all populations and all locations. The existence of a population-by-location interaction precluded presenting heritabilities over locations. Yield data are still being analyzed, but the narrow range of percent 110 recovered would limit the amount of yield response expected.

The interrelationship of the two traits included in this study has been examined in the past. Kvien et al. (1981) concluded that a line's recovery of strain 110 under field conditions was independent of the line's nodulation ability with the native rhizobia. In the present study, population 1 had the highest nodule mass/plant at all three locations, but showed the lowest recoveries of strain 110 across all three locations. Population 2 rated the poorest for nodule mass at Rosemount and St. Paul, but showed the highest recoveries of strain 110 at these two locations. However, correlations between nodule mass and the recovery of strain 110 were not statistically significant at any of the three locations.

Conclusions: Use of the visual rating system for improving nodule mass and the high heritabilities associated with its use offer hope for increasing the nodulation ability of lines currently being developed in breeding programs. The large environmental variances associated with the recovery of

Table 1. Estimates of mean, range, variances (phenotypic, genotypic, environmental) and heritability for nodule mass of uninoculated rows of soybeans

					Variances			
Character	Location	Population	Mean± S.E.	Range	Phenotypic	Genotypic	Environ.	Heritability
Nodule mass per plant*	Becker	1	3.30 ± .12	2.0-6.0	1.100	.129	.974	34.63
		2	2.77 ± .07	1.0-5.0	.961	.218	.743	53.99
		3	2.76 ± .08	1.0-6.0	.720	.157	.563	52.75
	Rosemount	1	2.15 ± .10	1.0-4.0	.803	.121	.682	41.51
		2	1.89 ± .06	1.0-4.0	.710	.229	.481	65.55
		3	1.94 ± .08	1.0-4.0	.699	.134	.565	48.62
	St. Paul	1	2.09 ± .11	1.0-5.0	.914	-.022	.935	≃ 0.00
		2	1.60 ± .06	1.0-4.0	.533	.165	.368	64.20
		3	2.03 ± .08	1.0-4.0	.746	.067	.679	28.12

*(1 = low nodule mass, 6 = high nodule mass).

Table 2. Estimates of mean, range, variances (phenotypic, genotypic, environmental) and heritability for recovery of strain 110 of *Rhizobium japonicum*

					Variances			
Character	Location	Population	Mean ±S.E.	Range	Phenotypic	Genotypic	Environ.	Heritability
		1	7.47 ± .68	0.0–31.3	36.69	-2.09	38.78	≈0.00
	Becker	2	9.02 ± .48	0.0–31.3	41.81	-0.26	42.07	≈0.00
		3	9.92 ± .61	0.0–31.3	46.66	6.66	40.00	39.96
		1	7.64 ± .87	0.0–26.7	27.47	-4.66	32.13	≈0.00
Recovery of strain 110*	Rosemount	2	9.34 ± .54	0.0–21.4	24.23	2.42	21.81	30.73
		3	8.95 ± .58	0.0–25.0	19.27	0.55	18.72	10.50
		1	10.23 ± .87	0.0–20.0	24.74	6.09	18.65	56.65
	St. Paul	2	11.31 ± .73	0.0–31.3	47.14	0.88	46.25	7.13
		3	11.21 ± .75	0.0–25.0	37.16	-1.49	38.65	≈0.00

* % of nodules containing strain 110

strain 110 and the low recoveries observed may limit the progress in selection for this trait. The choice of location in which to screen genotypes for genetic variability for traits associated with nitrogen fixation is an important determinant of the amount of improvement that can be realized.

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2) 245 Effect of seed production environment on genetic differences in cold tolerance during germination

Genetic variability for cold tolerance in soybeans has been reported by a number of researchers (Hillsman et al., 1977; Holmberg, 1973; Hume and Jackson, 1981; Hwang, 1979; Lambert, 1978, Littlejohns and Tanner, 1976; Spehar, 1977). Selection experiments for cold tolerance generally have pursued either vigorous germination and emergence or success in flowering and pod set. Neither is fully understood, although they appear to be independent of each other (Holmberg, 1973; Hume, personal communication). Examination of results of previous studies reveals that rank order changes among studies are not uncommon. This report summarizes some of our work in attempting to assess possible environmental effects on the prediction of genetic differences in germination cold tolerance.

We took 20 genotypes and grew them in five locations in Minnesota (St. Paul, Rosemount, Waseca, Lamberton and Morris) in 1981 and 1982. The genotypes used are listed in Table 1. Most of the named varieties have been grown in Minnesota at some time during the last 30 years, except 'Fiskeby V', a Swedish variety selected for superior cold tolerance during flowering and pod set, and 'Salut 216', a Russian variety reported by some to be cold tolerant. II-62-173 is a Minnesota line reported to have cold tolerance during emergence (Lambert, 1978). The PI lines were chosen based on their cold tolerance ratings by Spehar (1977), and based on differences in percent protein, percent oil or seedweight after USDA data. Spehar reported

Table 1. Soybean genotypes tested, their maturity groups and mean values obtained for germination index (with standard deviation and ranks), percent protein, percent oil, and hundred seedweight in grams

Genotype	M.G.	G.I.	Std. dev.	Rank	Prot.	Oil	Sdwt.
Altona	00	11.67	3.13	17	43.12	18.22	15.67
Blackhawk	I	8.13	2.09	3	41.66	18.19	15.08
Clay	0	9.56	3.32	11	41.91	19.13	14.88
Evans	0	11.51	2.66	18	41.66	18.38	14.23
Fiskeby V	000	12.70	3.24	20	42.21	18.58	14.28
Grande	0	12.12	2.97	19	40.04	18.13	20.84
Grant	0	8.97	2.72	6	42.04	17.60	15.48
Hodgson 78	I	10.51	3.15	12	41.89	18.66	15.82
McCall	00	8.72	2.28	5	40.12	18.84	13.25
Salut 216	00	9.44	2.47	9	42.31	18.30	13.21
Swift	0	9.28	2.72	7	40.37	18.23	15.28
II-62-173	0	9.28	2.62	8	41.60	18.57	13.13
PI 89001	0	10.88	3.06	13	43.24	17.49	19.40
PI 153320	0	9.57	2.76	10	42.96	18.38	14.90
PI 180507	00	7.32	2.91	1	44.58	18.94	14.77
PI 229330	0	11.83	3.63	16	47.71	13.52	10.33
PI 248401	0	10.91	2.91	14	44.09	16.84	13.70
PI 257432	0	8.41	2.49	4	42.85	17.41	13.48
PI 257433	0	7.57	2.02	2	42.45	18.24	14.01
PI 258384	0	11.09	3.43	15	43.12	17.50	15.06

that PI 89001 and PI 258384 were slow cold germinators, and PI 229330, PI 248401, PI 257432 and PI 257433 were fast cold germinators. PI 180507 was rated as only slightly faster than average, but was a significant outlier from the regression of protein on oil.

Fifteen live seeds from seed samples collected in each environment were put in petri dishes containing 60 g sand and 30 ml water within a growth chamber held at 10°C. A germination index (hereafter G.I.) was calculated based on the number of days for the first 10 seeds to have the radicle break through the testa:

$$\text{G.I.} = \sum \frac{(\text{no. seeds newly germ'd})(\text{no. days to that reading})}{(\text{total no. seeds germ'd with that reading})}.$$

Three replications were run. Percent protein, percent oil and hundred-seed weight were also obtained from the seed samples.

Analyses of variance for seed from each environment (location and year) showed that significant differences among genotypes existed for the G.I. from every environment except one (Waseca in 1982) which had experienced a severe drought. Combined analyses of variance revealed highly significant differences both years for genotypes and the genotype x location effect. Locations were significant in 1982 but not in 1981. Year had a nonsignificant effect.

Large rank order changes in the genotype G.I. values were common among seed from different environments. Correlations among means of genotypes for each environment are shown in Table 2. Seventeen of the 45 possible correlations were significant, although many of these had small r^2 values. We also regressed the mean values for each of the 1982 environments on the mean values for the 1981 environments. Of the 25 possible regressions, only two were significant. This ambiguity across environments is also reflected in the very large standard deviation values for the G.I. means based on seed from all ten environments (Table 1). Looking at Table 1, it can also be noted that PI 180507, PI 229330,PI 248401 and Salut 216 all performed differently than reported in other studies.

Table 2. Correlation coefficients among soybean genotypes from different environments

	RO81	WA81	LA81	MO81	STP82	RO82	WA82	LA82	MO82
STP81	.62**	.17	.48*	.15	.34	.23	.10	.27	.19
RO81		.32	.40	.19	.22	.25	.49*	.23	.49*
WA81			.27	.56**	.22	.09	.36	.39	.49*
LA81				.38	.41	.54*	.36	.64**	.47*
MO81					.18	.44*	.46*	.73**	.60**
STP82						.46*	.42	.20	.25
RO82							.65**	.48*	.31
WA82								.43	.51*
LA82									.62**

*,**Denote significance at .05 and .01 levels of probability, respectively.

STP = St. Paul; RO = Rosemount; WA = Waseca; LA = Lamberton; MO = Morris.

Our regressions between G.I. values and percent protein and hundred-seed weight were nonsignificant, and the regression between G.I. and percent oil was significant (r^2 = 0.017, however). Hwang (1979) reported similar results. It is interesting that the fastest germinator on a mean basis was also the outlier for high protein with high oil.

In line with others' reports, there is no apparent relationship between maturity group and germination cold tolerance. The poor performance of Fiskeby V tends to buttress the hypothesis that summer and spring cold tolerance are independent.

When the mean genotype values over all 1981 locations were used to predict the mean values over all 1982 locations, the regression was highly significant (r^2 = 0.56). In another study, not discussed further here, we compared percent emergence, an Emergence Index (E.I.), height and dry weight under early spring planting conditions with G.I. values, and found no significant correlations for G.I. values from any one seed source environment, but some significant correlations (for the E.I.) when G.I. values were the means over all seed source environments. Thus, we conclude that germination cold tolerance needs to be evaluated with seed from multiple seed production environments to be of reliable predictive value for any genetic differences in cold tolerance.

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1) 945 Screening for cyst nematode resistance in soybean breeding

As the soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, has become a serious pest of soybeans in the USA, development of resistant cultivars has received greater attention. This necessitates screening of large numbers of plant progenies to locate SCN-resistant isolates in segregating generations. Ross and Brim (1957) used a double-row method to detect SCN-resistant strains of soybeans. The conventional method of screening now involves growing one or two plants in a small pot containing soil adequately infested with SCN. After 30 days, the plant roots are exposed by gently shaking to remove the soil and then counting white females (cysts) on the roots. The plants are scored 0 through 4 based on the number of cysts on the roots of a plant (Epps and Hartwig, 1972); 0: no cyst, 1: 1-5 cysts, 2: 6-10 cysts, 3: 11-30 cysts and 4: 30+ cysts. In field screening, the plant rows are scored 1 through 5 for yellow appearance, plant height and poor yield performances. During the course of our screening for SCN, we have encountered several difficulties which lead us to try various methods seeking repeatable results. Here we report some of the common problems in screening for SCN and how we dealt with them.

Greenhouse screening

Level of inoculum: Inoculum containing an adequate number of cysts with viable eggs and larvae is most necessary for greenhouse screening. Ordinarily, infested soil is collected from a problem field in the fall and cyst counts are made for soil samples. An elutriator is used to extract the cysts. Cysts with viable eggs and larvae sink to the bottom. Cysts which float are devoid of or have few eggs. To determine the number of cysts needed for screening, a test was conducted with four inoculum levels of a mixture of races on two soybean varieties. The results are given in Table 1.

Table 1. Number of cyst nematodes on roots per plant (mean of 6 plants)

	Cyst infestation/100 g of soil				
Cultivar	5	10	20	30	40
Essex	26	52	61	77	86
Forrest	20	31	52	78	88

At least 10 good cysts per 100 g of soil are needed for proper screening. If inoculum potential is low, the number of cysts per unit of soil can be increased by growing a mixture of two or more susceptible varieties in greenhouse soil for about 35 days. Under good temperature and moisture conditions, the cyst number will increase from 10 to 100 per 100 g of soil in one

generation. A very high level of inoculum may distort the results. A high inoculum level can be satisfactorily diluted by mixing with sterile soil. Our results indicated that 20-30 cysts per 100 g of soil were best inoculum for pot screening.

Temperature: Temperature has a pronounced effect on SCN larval emergence and development (Slack and Hamblen, 1961; Ross, 1964). Our best results were obtained when plants were grown at 27.5°C. At a lower temperature, a longer time was required to complete the life cycle. At temperatures above 27.5°C, there were fewer cysts on the roots although the white cysts appeared earlier. Cyst development was reduced drastically when temperatures went above 35°C.

Number of days for SCN development: To determine the number of days required for SCN development and an optimum period required for scoring, the cultivar 'Essex' was grown in the greenhouse in SCN-infested soil at 27.5°C (± 1°C). Cysts were removed from the roots by a strong jet of water on an 80 mesh sieve. Cyst count was made by using a stereoscopic microscope. The data are presented in Table 2.

Table 2. Number of cyst nematodes on roots/plant (variety Essex: mean of 3 plants)

	Days after planting					
	20	24	26	28	30	35
Cyst number/plant	9	79	276	160	120	96

Cysts first appeared on roots 20 days after seeds were planted. The number of cysts increased for 6 consecutive days, but decreased thereafter. Since seedlings take 6-8 days to develop an adequate root system, 26 days are required to produce maximum root infestation for optimum observation at 27.5°C. The decline of cyst after that period is due to falling off of the cysts from the roots.

Black seed coat: Several of the resistant soybean PI lines which are used in breeding programs are black seeded and have poor germination if seeded directly. Similar problem is encountered in the black-seeded segregates following hybridization. To increase germination, the seed was scarified (a) with a knife and (b) by swirling vigorously for a minute in a beaker with 150-grade sandpaper all around. The data are presented in Table 3. Scarification by either method improved germination of black-coated seed. Scarification of individual seed with a knife did a better job than did scarification with sandpaper; however, it involved longer time.

Table 3. Effect of scarification on seed germination

Genotype	Percent germination (7 days after planting) Control	Scarified with knife	Scarified with paper
PI 88788	62	86	78
PI 89772	52	80	72

Field Screening

Level of inoculum: The most difficult problem in field screening is the development and maintenance of a uniformly high inoculum potential in the soil, which is very necessary. The inoculum level can be increased up to 20 times during the season by growing a susceptible variety. It may increase little if a variety resistant to one or more races of SCN is grown (Anand, 1981). Thus, the inoculum level will vary with the level of resistance of the previously grown variety. Therefore, it is necessary to grow one or more susceptible varieties uniformly in the test field the preceding year. Planting soybeans in narrow rows aids rapid inoculum increase. A healthy crop stimulates SCN development. A poor crop due to drought or very low fertility may decrease the cyst count. It would also be desirable to establish cyst nursery in a field with uniform soil type. In light sandy soils, cysts develop well and are preferred over loam soils for nursery plots. Heavy soils are not suitable for SCN development.

Time of screening: SCN has no effect on the germination and stand of the crop. Early field symptoms appear about 4 weeks after planting. Susceptible lines are slightly shorter and have yellowish leaves, typical symptoms of nitrogen deficiency. Leaf yellowing is less pronounced later. The best time for scoring SCN resistance appears to be about 6 weeks after planting. Droughty conditions aggravate expression of susceptible symptoms whereas heavy rains have an opposite effect. Lines can be evaluated again at maturity, based on plant height and general performance. Field scores are recorded as 1 through 5. One is considered highly resistant and 5 highly susceptible with no seed production. Check cultivars grown at regular intervals (1 in 10 rows) provide a measure of SCN infestation in the field.

Comparison of greenhouse and field screening

Eighty-one advance lines were screened in the greenhouse and in the field cyst nursery. Scoring by the two procedures was highly correlated ($r = .63^{**}$) indicating that both the methods gave similar results.

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1) 245 Inheritance of soybean electrophoretic variants.

We have been using the technique of slab-gel electrophoresis (see Gorman and Kiang, 1977, 1978; Kiang, 1981; Kiang and Gorman, 1983, for methods) to study genetic diversity in *G. max* and *G. soja*. In last year's Soybean Genetics Newsletter, we reported the accession-specific zymogram types (zymogram types are equivalent to phenotypes) observed in 253 named cultivars (maturity groups 00-IV) for 15 enzyme systems (Gorman et al., 1982b). We have been studying the genetic basis for the differences between these zymogram types. The purpose of this report is to present some of our data concerning the genetic inheritance for electrophoretic variants in eight of these 15 enzyme systems and to designate appropriate gene symbols. The inheritance of variants in five of the other enzyme systems have been reported previously (Hildebrand et al., 1980; Hildebrand and Hymowitz, 1980; Buzzell and Buttery, 1969; Gorman and Kiang, 1978; and Kiang, 1981), while two enzyme systems were invariant (Gorman et al., 1982a).

For convenience and uniformity, we have now numbered each accession-specific (homozygous) zymogram type (Fig. 1). Nonaccession-specific (heterozygous) zymograms have been labeled collectively as H type. Thus, the zymogram classifications we reported last year are changed as follows: Am: F = 1, S = 2, S^w = 3, N = 4; AP: F = 1, M = 2, S = 3; LAP: F = 1, S = 2; MPI: F = 1, M = 2, S = 3, N = 5; PGM: PF = 1, PS = 2.

A) Diaphorase (Dia): Dia zymograms in soybeans are quite complex (Fig. 1A), with as many as 12 anodal bands visible in some tissues. We found that the Dia zymograms observed in 402 *G. max* cultivars and accessions of 67 *G. soja* accessions were delineated by four distinct electrophoretic variants. The first of these Dia variants affected the expression of a cluster of five bands with R_f's of .19, .22, .25, .28 and .31 (R_f = distance of enzyme bands/distance of methyl violet). With respect to these five bands, there were two accession-specific zymogram types. In the first, the R_f .19 band was the weakest, while the other four bands increased in intensity slightly with mobility (odd numbered zymograms in Fig. 1A). The second type had the R_f .19 band with the greatest intensity, while the other four bands decreased in intensity with mobility, so that the R_f .28 and .31 bands were generally not visible (even numbered zymograms in Fig. 1A). We hypothesize that these variant zymogram types result from a single locus with two variant incompletely dominant alleles. A 1:2:1 F_2-segregation ratio (Table 1) was observed in crosses between the accession-specific zymogram types. Heterozygotes (H type in Fig. 1A) displayed a nonaccession-specific zymogram in which all five bands had relatively equal strength. Only seeds with the H-type zymogram in the F_2 generation segregated in the F_3, and there was no difference between reciprocal crosses. We designate the locus involved as Di_1, with the variant alleles Di_1 and di_1. The di_1

allele, when homozygous, produced the even numbered zymogram types in Fig. 1A, and the *Di_1* allele the odd numbered zymogram types.

The second Dia electrophoretic variant involved the mobility of the seventh and eighth Dia bands with two accession-specific zymograms observed. In the first (zymogram types 1,2,7,8,9,10,15 and 16 in Fig. 1A) the two bands had a migration rate of R_f .46 and .51, and in the second (zymogram types 3, 4,5,6,11,12,13 and 14 in Fig. 1A) they had a mobility of R_f .41 and .47. We hypothesize that a single locus with two variant codominant alleles is responsible for the difference. In crosses between the two, a 1:2:1 F_2-segregation ratio was observed (Table 1). Heterozygotes displayed a nonaccession-specific zymogram (H type in Fig. 1A) in which both parental bands were seen. Only F_2 seeds showing the H-type zymogram segregated in the F_3 generation. There was no difference between reciprocal crosses. We designate the locus involved with this electrophoretic Dia variant Di_2, with the variant codominant alleles Di_2^f (producing the bands at R_f .46 and .51) and Di_2^s (producing the bands at R_f .41 and .47).

The third Dia electrophoretic variant had two accession-specific zymogram types differing in the presence or absence of the R_f .62 Dia band. We hypothesize a single locus with variant dominant and recessive alleles as responsible for the difference. In crossing the two types, a 3 (R_f .62 band present):1 (R_f .62 band absent) F_2-segregation ratio was observed, with no difference between reciprocals (Table 1). We designate the locus Di_3 with the dominant allele Di_3 and the recessive allele di_3.

The cross of the cultivars 'Elton' and 'Kingston' segregates for all three variable Dia loci. The data collected from this cross is consistent with a model of three distinct Dia variable loci, as all of the 18 expected phenotypic classes have been observed.

We have no genetic data concerning the fourth variant Dia electrophoretic type. Accessions fixed for the fourth variant lacked the two fastest migrating (R_f .68 and .75) bands (zymogram types 9-16 in Fig. 1A).

B) Glucose-6-phosphate dehydrogenase (GPD): Two accession-specific GPD zymogram types were observed in the 436 *G. max* and 111 *G. soja* accessions and cultivars tested (Fig. 1B). They differed in the staining intensity of three cytoplasmic GPD bands with R_f's of .30, .35 and .41, particularly differing in the R_f .35 and .41 band's intensities. Enzyme assays confirmed that the low (type 1 in Fig. 1B) and high (type 2 in Fig. 1B) intensity zymogram types also differed in the amount of GPD activity/mg extracted protein. We hypothesize that the two types are controlled by a single nuclear locus with two variant alleles, the high intensity type apparently being dominant. In crosses between the two types, the F_2 and segregating F_3 families had a 3 type-2:1 type-1 segregation ratio (Table 2). However, since zymograms were only examined visually, it was possible that heterozygotes could have had an intermediate intensity. There was no difference between reciprocal crosses. The type-1 F_2 seeds bred true, but approximately 2/3 of the type-2 F_2 seeds segregated in the F_3 (Table 2). We designate the low intensity (type 1) allele *gpd* and the high intensity (type 2) allele *Gpd*.

C) NADP-active isocitrate dehydrogenase (IDH): NADP-active IDH-zymogram differences were first reported in soybeans by Yong et al. (1981). Gorman et al. (1982b) subsequently reported additional types. Yong et al. found four homozygous zymogram types, three (types 1+2, 3+4, and 7+8 in Fig. 1C) with three band patterns that differed in band mobilities, and one (type 5+6 in Fig. 1C) with a single band. They did not do a complete inheritance study, but concluded that the three-band zymograms were the consequence of a newly duplicated pair of variable loci, while the one-band type represented a nonduplicated line with only a single active locus. Our conclusions differ from those of Yong et al. We found in inheritance studies that the single-band zymogram type, when crossed with zymogram types 3 or 4 (Fig. 1C), showed a dihybrid, both loci with two codominant alleles, segregation ratio (Table 3). This indicated that both of the loci active in the three-band zymogram types also were active in the single band type. We hypothesize that the four homozygous zymogram types reported by Yong et al. are delineated by two interacting (their monomers combine into dimers) loci, each having a pair of codominant alleles. Each allele produces an IDH monomer with a different electrophoretic mobility, except that the product of one of the alleles at the first locus has the same migration rate (R_f .56) as the product of one of the alleles at the second locus. Individuals homozygous for both of these alleles have the zymogram types with only a single visible band (types 5 and 6 in Fig. 1C). Monomers of the remaining two alleles have migration rates of R_f .63 and .49, resulting in three-band zymograms (two homodimers plus an interlocus heterodimer) for the other three homozygous allele combinations at the two loci. If this hypothesis is correct, then the F_2 dihybrid phenotypic ratio would be expected to be distorted from a 4:2:2:2:1:1:1:2:1 ratio to a 8:3:1:1:3 ratio as some of the genotypic classes become indistinguishable. The theoretical demonstration of this is beyond the scope of this report. We have observed an 8:3:1:1:3 F_2 ratio on all possible dihybrid crosses (Table 3). Neither this observed ratio nor the observed F_2-and F_1-zymogram types fit what would be expected under Yong et al.'s hypothesis. F_2-progeny tests revealed the expected genotypic ratio for a dihybrid cross (Table 3). Individuals with various heterozygous combinations showed the parental bands as well as two intermediate (R_f .60 and .53) hybrid dimer bands. F_2 seeds with this 5-band (H-type) zymogram always segregated in the F_3 generation, but, as expected with this model, in three different ways (Table 3). The segregation ratios and zymograms observed indicated that the monomers produced by all alleles combined randomly to form all expected intra- and inter-locus dimers. We designate the two loci Idh_1 and Idh_2, with the respective codominant variant alleles Idh_1^f, Idh_1^s, Idh_2^f and Idh_2^s. The monomers of the Idh_1^f and Idh_2^s alleles have the same migration rate.

The additional IDH zymogram variant types we reported (Gorman et al., 1982b) involve the mobility of one of two bands found from cell fractionation studies to be associated with mitochondria. These variants are distinct from the previously discussed IDH variants which concern cytoplasmic associated IDH isozymes. Three accession-specific types, with bands at R_f .31 (types 2,4,6 and 8 in Fig. 1C), .37 (types 1,3,5 and 7 in Fig. 1C) or .41 (types 9-12 in Fig. 1C), have been observed in the 403 *G. max* and 70 *G. soja* cultivars and accessions tested to date for IDH zymogram types. We hypothesize that a single locus with variant codominant alleles controls the difference. We studied the inheritance using crosses involving only two of the zymogram variants, finding that F_2 seeds showed a 1:2:1 segregation

ratio (Table 4). Heterozygotes (H-type) displayed both parental bands, although, due to the weak staining of these bands, they were hard to score, so that seeds scored as heterozygotes in the F_2 usually segregated in the F_3, but some mistaken scores were evident (Table 4 is the corrected data). Seeds with the R_f .31 band (zymogram types 2, 4, 6 and 8) were easier to score and always bred true. There was no difference between reciprocal crosses. We designate the locus as Idh_3 with the two tested variable alleles $Idh_3{}^s$ (producing the R_f .31 band) and $Idh_3{}^m$ (producing the R_f .37 band).

The cross between the cultivars 'Amsoy' and 'Wilson' segregates for all three variable IDH loci and all 15 expected phenotypic classes have been observed.

D) Leucine amino peptidase (LAP): A total of four accession-specific LAP zymogram types have been observed in the 425 *G. max* and 131 *G. soja* accessions and cultivars examined. Zymogram types 1, 2 and 3 (Fig. 1D) had two anodal LAP bands differing in the mobility (R_f's .49, .53 and .58) of the first LAP band, while type-4 zymograms lacked the second LAP band. The difference between the types 1 and 2 zymograms is hypothesized to be controlled by a single nuclear gene with two codominant alleles. A 1:2:1 F_2-segregation ratio was observed in crosses between types 1 and 2 plants (Table 5). Heterozygotes showed both the R_f.49 and .53 bands. Only F_2 seeds with both bands (H type in Fig. 1D) segregated in the F_3, and there was no difference between reciprocal crosses. We designate the locus involved as *Lap* with the variable alleles Lap^f (producing the R_f .53 band) and Lap^s (producing the R_f .49 band).

E) Mannose-6-phosphate isomerase (MPI): Five accession-specific MPI zymogram types have been observed in the 403 *G. max* and 72 *G. soja* accessions and cultivars tested. Zymogram types 1, 2, 3 and 4 differed in their mobilities (R_f's of .58 and .64, .65 and .70, .71 and .75 and .76 and .81) of the only two MPI bands observed (Fig. 1E). The type-5 MPI zymogram showed weak-null MPI bands with a migration rate of R_f .65 and .70. We hypothesize that a single locus with variable codominant alleles is responsible for the mobility differences. Inheritance studies dealing with three of these types (types 1, 2 and 3 in Fig. 1E) showed a 1:2:1 segregation ratio from all crosses (Table 6). Heterozygotes (there were three different nonaccession-specific H-type zymograms) showed both sets of parental bands, and only H-type F_2 seeds segregated in the F_3. There was no difference in the one reciprocal cross tested. We designate the locus as *Mpi* with the codominant variable alleles Mpi^f (producing bands at R_f .71 and .75), Mpi^m (producing bands at R_f .65 and .70) and Mpi^s (producing bands at R_f .59 and .64).

F) Phosphogluconate dehydrogenase (PGD): We have observed four accession-specific PGD zymogram types in the 403 *G. max* and 71 *G. soja* accessions and cultivars tested. The variant zymogram types observed all involved three cytoplasmic associated bands. In types 1 and 2 zymograms, the mobility of two of the three bands differed (bands at R_f .22 and .25 vs. bands at .17 and .23), in type-3 zymograms these same two bands were absent and in type-4 zymograms, the mobility of all three bands was altered (Fig. 1F). We hypothesize that the types 1 and 2 variants are the result of two codominant alleles at a single nuclear locus, while the type-3 variant is the result of a recessive null allele at this same locus. We also hypothesize that these three cytoplasmic bands form a fixed homo-heterodimer complex produced by the variable locus interacting with a second locus (the

monomers of the two loci combine randomly to form two homodimer bands and one inter-locus heterodimer band). The monomers produced by the variable locus are thought to combine to form the slower migrating homodimer and contribute to the intermediate migrating interlocus heterodimer. As predicted with this model, a 1:2:1 F_2-segregation ratio was observed between crosses of type-1 and type-2 plants (Table 7), with heterozygotes showing the parental as well as a new intra-locus hybrid dimer band (H-type Fig. 1F). There was no difference between reciprocals. The crosses between type-1 and type-3 plants displayed a 3-bands-present:1-band-absent F_2-segregation ratio (Table 7). F_2 seeds from this cross having the type-3 zymogram bred true, but 6 of the 10 F_2 seeds tested with the type-1 zymogram segregated in the F_3. There was no difference between reciprocal crosses. We designate the variable locus as *Pgd* with the codominant alleles Pgd^f (producing the type-1 zymogram when homozygous), Pgd^s (producing the type-2 zymogram when homozygous) and the recessive allele *pgd* (producing the type-3 zymogram when homozygous).

G) Phosphoglucose isomerase (PGI): We have observed four accession-specific PGI zymogram types in the 428 *G. max* and 120 *G. soja* accessions and cultivars tested. Zymogram types 1, 2 and 3 (Fig. 1G) all had four anodal bands, but differed in their mobility of the two fastest migrating bands (R_f's .69 and .57, .63 and .54, and .59 and .52, respectively). Type-4 zymograms lacked the two fastest migrating bands. We hypothesize that the difference between the types 1 and 3 zymograms is controlled by a single nuclear gene with two codominant alleles. We also hypothesize that the products of the variable locus and of a second locus interact to form a fixed three-band homo-heterodimer complex, in which the monomers from the variable locus combine to produce the faster migrating homodimer, and contribute to the intermediate, inter-locus heterodimer. As predicted with this model, a 1:2:1 F_2-segregation ratio (Table 8) was observed in crosses between type-1 and type-3 plants. Heterozygotes displayed the parental bands as well as a new intra-locus hybrid dimer band. Only F_2 seeds with this heterozygous (H-type) zymogram segregated in the F_3, and there was no difference between reciprocal crosses. While we do not have genetic data, type-2 and type-4 zymograms are consistent with expectable variants under this genetic model. We designate the variable locus as *Pgi* with the two genetically confirmed alleles designated Pgi^f and Pgi^s. The Pgi^s allele when homozygous produced the type-3 zymogram and the Pgi^f allele when homozygous the type 1.

H) Phosphoglucomutase (PGM): We have observed four accession-specific PGM zymogram types in the 432 *G. max* and 124 *G. soja* accessions and cultivars tested (Fig. 1H). The difference in zymogram types was delineated by two different variants. The first involved the mobility of the slowest migrating PGM band. Two accession-specific zymograms (odd- vs. even-numbered zymograms in Fig. 1H) having a band either at R_f .54 or .51 were observed. This band was found in cell fractionation studies to be associated with plastids. We hypothesize a single nuclear locus with two variable codominant alleles as responsible for the difference. A 1:2:1 F_2 segregation ratio was observed in crosses between the two accession-specific types (Table 9). Heterozygotes displayed a nonaccession-specific zymogram (H-type in Fig. 1H) in which both the R_f .54 and .51 bands were seen. Only the H-type F_2 seeds segregated in the F_3. The Mendelian segregation ratio and the lack of maternal effect in reciprocal crosses (Table 9) indicates that the variable locus is nuclear despite its products' activity in plastids. We designate

the locus *Pgm_1* with the codominant alleles *Pgm_1^f* (producing the R_f .54 band) and *Pgm_1^s* (producing the R_f .51 band).

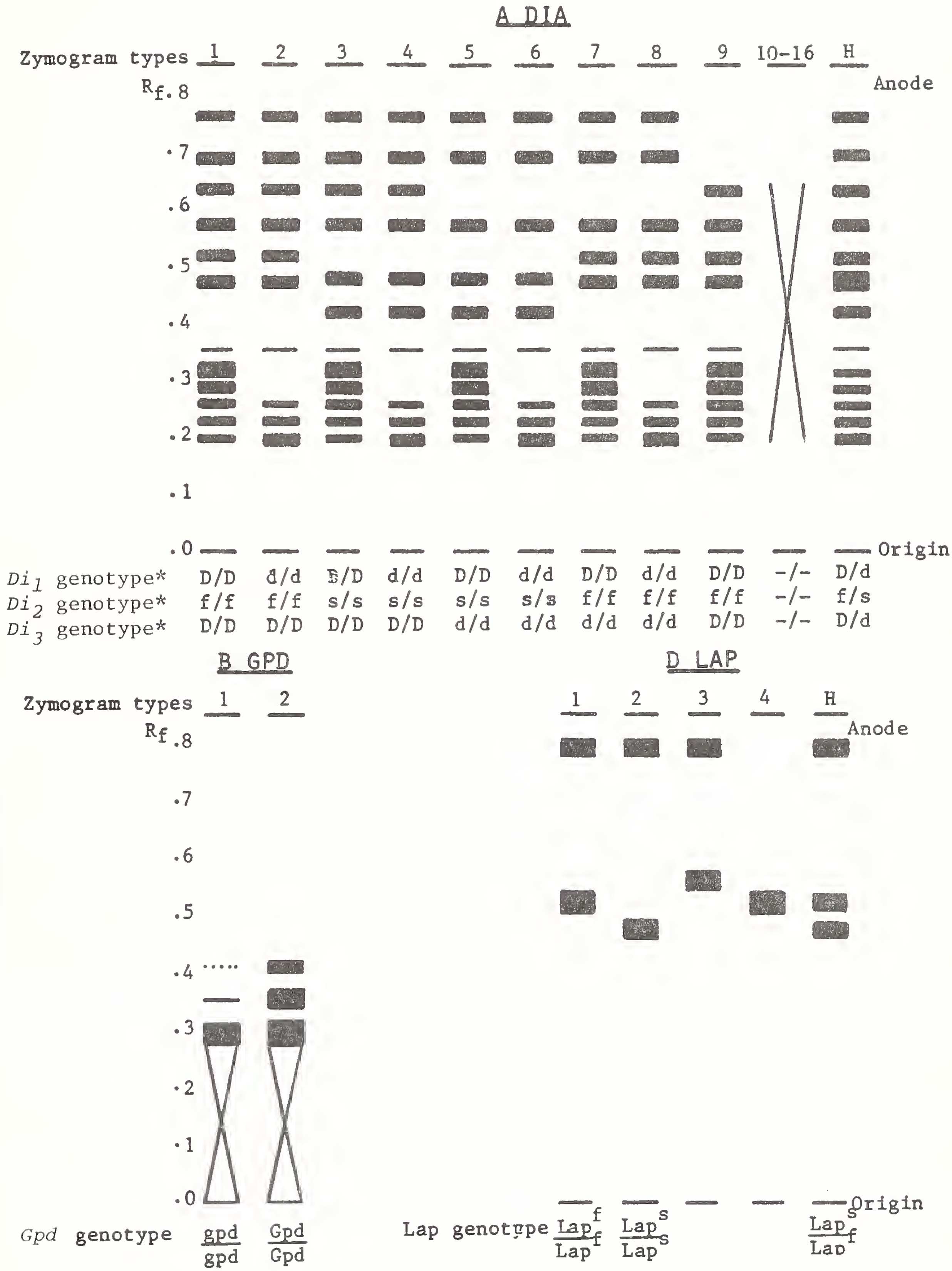
The second PGM electrophoretic variant had two accession-specific zymogram types (types 1 and 2 vs. 3 and 4 in Fig. 1H). The first had a strong band at R_f .69 and a weak band at R_f .74, while the second resulted in zymograms lacking the R_f .69 band and having a strong R_f .74 band. We hypothesize that a single locus with two variable alleles is responsible for the difference. In crosses between the two accession-specific zymograms, a 1:2:1 ratio was seen in segregating F_2 and F_3 seeds (Table 9). Heterozygotes displayed a nonaccession-specific zymogram (H-type in Fig. 1H) in which both bands were seen, but the R_f .74 band had the greater intensity. Only the F_2 seeds showing the H-type zymogram segregated in the F_3. There was no difference between reciprocal crosses. However, two hypotheses are still possible with regard to the type of alleles involved. The first is that the variant alleles are codominant and simply affect the mobility of the R_f .69 band. The second hypothesis, with recessive null and dominant functional alleles, can't be rejected if one also includes a regulatory effect upon the R_f .74 band with the alleles. With the first hypothesis, when one allele is homozygous, both the R_f .69 and .74 bands are visible and when the second allele is homozygous, the mobility of the slower band changes so that it corresponds in mobility with the R_f .74 band, resulting in a single strong band. When these two alleles are heterozygous, both bands are seen, but the R_f .69 band is weaker and the R_f .74 band stronger than the bands observed in the homozygous types 1 or 2 zymograms. We favor this first hypothesis as in some electrophoretic runs the R_f .74 band in types 3, 4 and H zymograms appears to consist of two closely migrating bands, but the separation is not distinct. We will designate the variable locus as *Pgm_2*, but not designate allele symbols at this time.

Crosses segregating for both PGM variable loci show all nine expected phenotypic (zymogram) types.

In accordance with the recommendations of the Soybean Genetics Committee, some of the gene symbols designated in this paper differed slightly from those previously used by us (Kiang and Gorman, 1983). The changes are as follows:

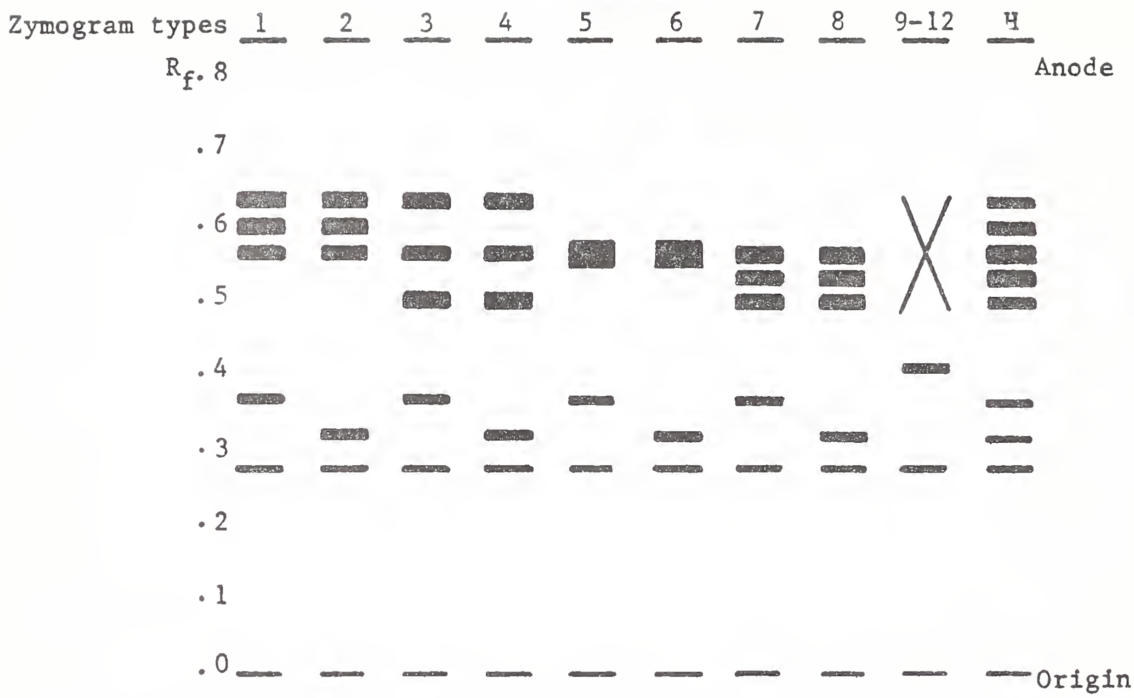
Di_1 for *Dia_1^+*, *di_1* for *dia_1^n*, *Di_2^f* for *Dia_2^f*, *Di_2^s* for *Dia_2^s*, *Di_3* for *Dia_3^+*, *di_3* for *dia_3^n*, *Gpd* for *Gpd_1^h*, *gpd* for *gpd_1^l*, *Lap^f* for *Lap_1^f*, *Lap^s* for *Lap_1^s*, *Mpi^f* for *Mpi_1^f*, *Mpi^m* for *Mpi_1^m*, *Mpi^s* for *Mpi_1^s*, *Pgd^f* for *Pgd_1^f*, *Pgd^s* for *Pgd_1^s*, *pgd* for *pgd_1^n*, *Pgi^f* for *Pgi_1^f*, *Pgi^s* for *Pgi_1^s*, and no allele symbols designated for the *Pgm_2* alleles.

FIGURE 1. OBSERVED ELECTROPHORETIC ZYMOGRAMS



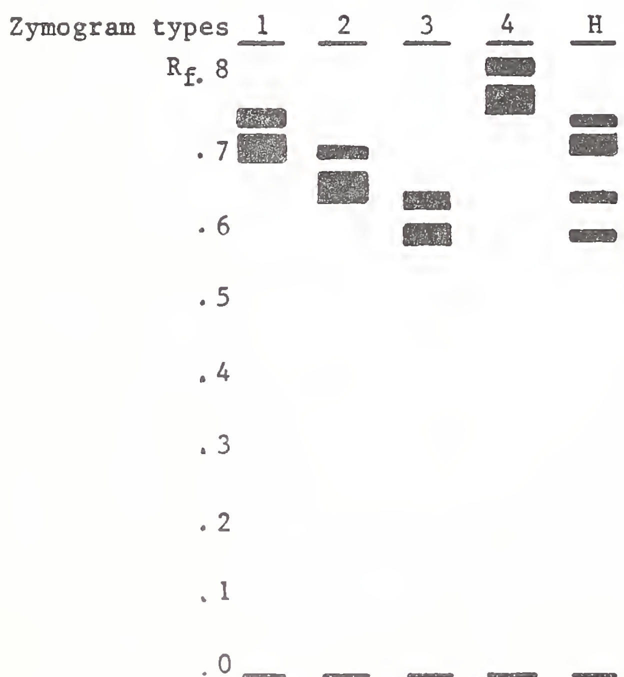
* Because of space limitations the Di_1 allele is symbolized as D, di_1 as d, $Di_2^{\,f}$ as f, $Di_2^{\,s}$ as s, Di_3 as D and di_3 as d.

C IDH



	1	2	3	4	5	6	7	8	9-12	H
Idh$_1$ genotype*	f/f	f/f	s/s	s/s	f/f	f/f	s/s	s/s	-/-	f/s
Idh$_2$ genotype*	f/f	f/f	f/f	f/f	s/s	s/s	s/s	s/s	-/-	f/s
Idh$_3$ genotype*	m/m	s/s	m/m	s/s	m/m	s/s	m/m	s/s	-/-	m/s

E MPI

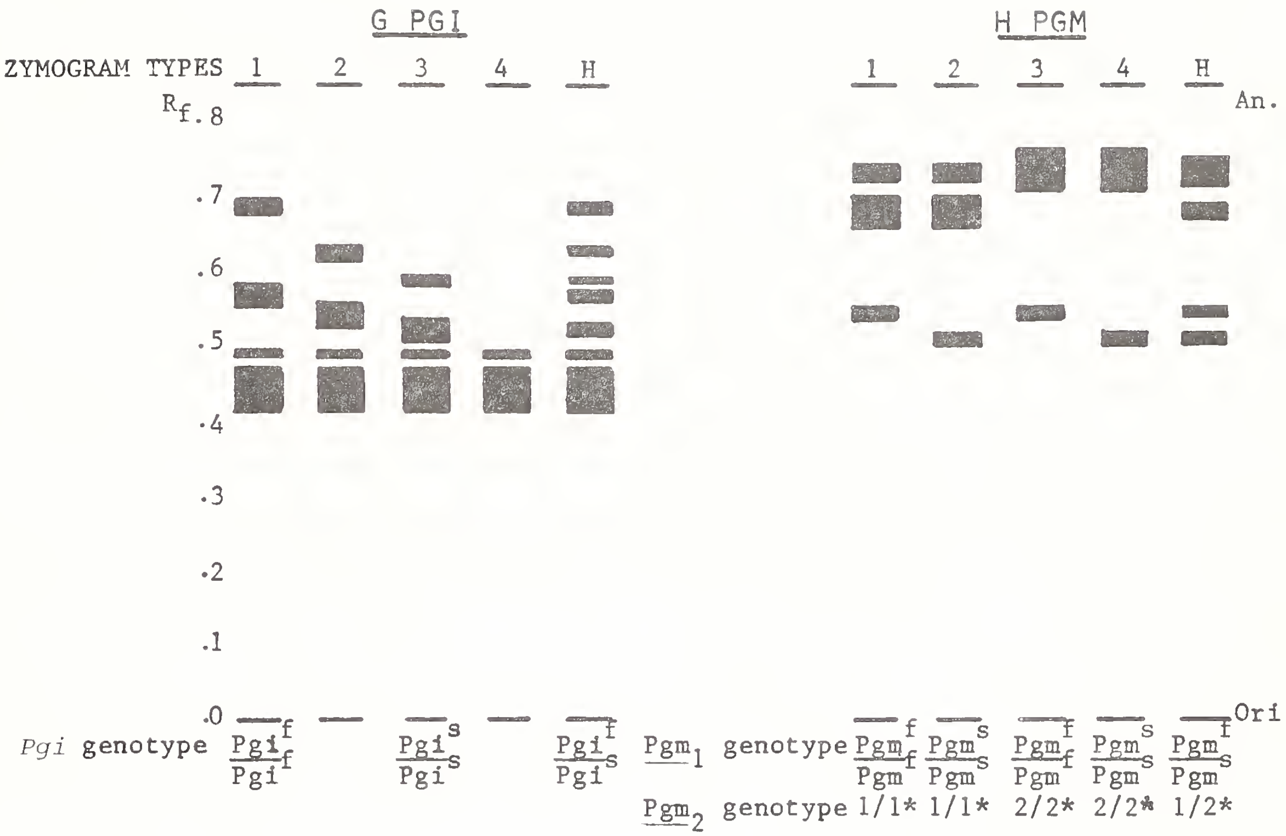


Mpi genotype $\frac{Mpi^f}{Mpi^f}$ $\frac{Mpi^m}{Mpi^m}$ $\frac{Mpi^s}{Mpi^s}$ $\frac{Mpi^f}{Mpi^s}$

F PGD

Pgd genotype $\frac{Pgd^f}{Pgd^f}$ $\frac{Pgd^s}{Pgd^s}$ $\frac{pgd}{pgd}$ $\frac{Pgd^f}{Pgd^s}$

* Because of space limitations only the superscripts of the allele symbols have been used for genotypes.



* Allele symbols for the Pgm_2 locus have not yet been designated, we used 1 and 2 to represent the two Pgm_2 alleles.

Figure 1: A) Diaphorase zymogram types as would be observed in dry seed cotyledons. B) Glucose-6-phosphate dehydrogenase zymogram types as would be observed in dry seed cotyledons. D) Leucine amino peptidase zymogram types, the slower band would be observed in dry seed cotyledons, but the upper band is seen only several days after germination at which point the lower band is lost. C) Isocitrate dehydrogenase zymogram types as would be observed in dry seed cotyledons. E) Mannose-6-phosphate isomerase type 1, 2, 3, 4 and one of the H (heterozygous for the Mpi^f and Mpi^s alleles) zymograms as would be observed in dry seed cotyledons, the type 5 zymogram is not pictured and is simply weak or absent type 2 bands. F) 6-phosphogluconate dehydrogenase zymogram types as would be observed in dry seed cotyledons. G) Phosphoglucose isomerase zymogram types as would be seen in dry seed cotyledons, but the R_f .5 band is primarily seen in green tissues. H) Phosphoglucomutase zymogram types as would be observed in dry seed cotyledons, although the R_f .50 and .54 bands are only weakly seen in this tissue. The X marks in the figures represent either bands extraneous to the discussion or repeated banding patterns. The R_f values are somewhat variable and should be used only as estimates.

Table 1. Inheritance of alleles at the soybean Di_1, Di_2 and Di_3 loci

Crosses	F_2 seeds and F_2 * plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1,3,5	H	2,4,6	1,3,5	H	2,4,6
Di_1 genotypes:	Di_1/Di	Di_1/di_1	di_1/di_1	Di_1/Di_1	Di_1/di_1	di_1/di_1
Cayuga X Evans Zymogram type 2 X 1 di_1/di_1 X Di_1/Di_1	16	37	22	17	25	16
PI 406684 X A73-109084 Zymogram type 2 X 1 di_1/di_1 X Di_1/Di_1	6	18	7	9	26	13
Elton X Kingston Zymogram type 5 X 4 Di_1/Di_1 X di_1/di_1	7	18	7			
Total observed:	29	73	36	26	51	29
χ^2 (expected 1:2:1) =		0.96 = n.s.			0.54 = n.s.	
Zymogram types:	1,2,5,6	H	3,4	1,2,5,6	H	3,4
Di_2 genotypes:	Di_2^f/Di_2^f	Di_2^f/Di_2^s	Di_2^s/Di_2^s	Di_2^f/Di_2^f	Di_2^f/Di_2^s	Di_2^s/Di_2^s
A73-25050 X PI 407195 Zymogram type 1 X 4 Di_2^f/Di_2^f X Di_2^s/Di_2^s	8	14	7	14	32	16
Amsoy X Wilson Zymogram type 1 X 4 Di_2^f/Di_2^f X Di_2^s/Di_2^s	14	45	31	32	67	37
Kingston X Elton Zymogram type 4 X 5 Di_2^s/Di_2^s X Di_2^f/Di_2^f	9	15	8			
Total observed:	41	74	46	46	99	53
χ^2 (expected 1:2:1) =		1.45 = n.s.			0.50 = n.s.	

*F_2 plant progenies and F_2 seeds were the same except for those F_2 seeds which did not germinate, since the electrophoretic technique is nondestructive allowing progeny tests on the same F_2 seeds.

Table 1. *Continued*

Crosses	F_2 seeds	
Zymogram types:	1,2,3,4	5,6
Di_3 genotypes:	$\frac{Di_3}{-}$	$\frac{di_3}{di_3}$
Agate X Elton Zymogram type 1 X 5 Di_3/Di_3 X di_3/di_3	35	12
Elton X Kingston Zymogram type 5 X 4 di_3/di_3 X Di_3/Di_3	22	10
Total observed:	57	22
χ^2 (expected 3:1) =	0.35 = n.s.	

PI's 406684 and 407195 are *G. soja* accessions, while A73-109084 and A73-25050 are experimental *G. max* lines.

Table 2. Inheritance of alleles at the soybean *Gpd* locus

Crosses	F_2 seeds		F_2 plant progenies			F_3 seeds from segregating F_2 plants	
Zymogram types:	2	1	2	Seg	1	2	1
Gpd genotypes:	$\frac{Gpd}{-}$	$\frac{gpd}{gpd}$	$\frac{Gpd}{Gpd}$	$\frac{Gpd}{gpd}$	$\frac{gpd}{gpd}$	$\frac{Gpd}{-}$	$\frac{gpd}{gpd}$
Cayuga X Evans Zymogram type 1 X 2 *gpd/gpd* X *Gpd/Gpd*	57	18	4	6	2	52	18
Chestnut X Amsoy Zymogram type 1 X 2 *gpd/gpd* X *Gpd/Gpd*			6	12	3	127	48
Amsoy X Wilson Zymogram type 2 X 1 *Gpd/Gpd* X *gpd/gpd*	74	24	9	15	6	66	25
Total observed:	131	42	19	33	11	245	91
χ^2(3:1, 1:2:1, 3:1) =	0.05 = n.s.		2.12 = n.s.			0.77 = n.s.	

Seg equals segregating in the F_3 generation.

Table 3. Inheritance of alleles at the soybean Idh_1 and Idh_2 loci. Data from crosses segregating for both loci

	F_2 segregation: F_3 seeds from dihybrid F_2						F_2 genotypes obtained from progeny tests[†]						
						F_2 zymo:	H type			type 1,2		type 7,8	
Zymogram types:	H	1,2	3,4	5,6	7,8	F_3 zymo:	All	H,1,2,3,4	H,3,4,7,8	1,2,5,6	1,2	5,6,7,8	7,8
Genotype locus 1:*	s/-	f/f	s/s	f/f	s/-		f/s	f/s	s/s	f/f	f/f	s/s	s/s
Genotype locus 2:*	-/f	f/-	f/f	s/s	s/s		f/s	f/f	f/s	f/s	f/f	f/s	s/s
Crosses													
Chestnut X Amsoy													
Idh_1 f/f X s/s *	10	2	2	1	4		5	1	4	1	1	3	1
Idh_2 f/f X s/s *	74	30	15	10	32								
Amsoy X Wilson													
Idh_1 s/s X f/f *	50	19	4	5	15		14	8	4	7	3	4	1
Idh_2 s/s X f/f *	34	11	6	4	9								
Cayuga X Evans													
Idh_1 s/s X f/f *	77	31	14	9	28		4	1	1	3	2		1
Idh_2 s/s X f/f *	39	17	5	6	14								
Agate X Elton													
Idh_1 f/f X s/s *	34	16	6	4	16								
Idh_2 s/s X f/f *													
Total observed:	318	126	53	39	118		23	10	9	11	6	7	3[†]
Expected ratio 8:3:1:1:3 χ^2 = 4.20 = n.s.							Expected ratio 4:2:2:2:1:2:1:1:1 χ^2 = 4.90 = n.s.						

*Only the superscript of the allele symbols are given because of space limitations.

[†]The 4 type 3+4 (Idh_1^s/Idh_1^s, Idh_2^f/Idh_2^f) and the 2 type 5+6 (Idh_1^f/Idh_1^f, Idh_2^s/Idh_2^s) F_2 seeds in the progeny test bred true.

Table 4. Inheritance of alleles at the soybean *Idh*$_3$ locus

Crosses	F_2 seeds and F_2* plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1,3,5,7	H	2,4,6,8	1,3,5,7	H	2,4,6,8
Idh$_3$ genotypes:	$\frac{Idh_3^m}{Idh_3^m}$	$\frac{Idh_3^m}{Idh_3^s}$	$\frac{Idh_3^s}{Idh_3^s}$	$\frac{Idh_3^m}{Idh_3^m}$	$\frac{Idh_3^m}{Idh_3^s}$	$\frac{Idh_3^s}{Idh_3^s}$
Amsoy X Wilson Zymogram type 8 X 1 Idh_3^s/Idh_3^s X Idh_3^m/Idh_3^m	21	48	23	24	44	25
Agate & Kingston X Elton Zymogram type 5&3 X 4 Idh_3^m/Idh_3^m X Idh_3^s/Idh_3^s	24	39	16			
Total observed:	45	87	39	24	44	25
χ^2 (expected 1:2:1) =		0.58 = n.s.			0.28 = n.s.	

Table 5. Inheritance of alleles at the *Lap* locus in soybeans

Crosses	F_2 seeds and F_2 plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1	H	2	1	H	2
Lap genotypes:	$\frac{Lap^f}{Lap^f}$	$\frac{Lap^f}{Lap^s}$	$\frac{Lap^s}{Lap^s}$	$\frac{Lap^f}{Lap^f}$	$\frac{Lap^f}{Lap^s}$	$\frac{Lap^s}{Lap^s}$
Lindarin X Norredo Zymogram type 1 X 2 Lap^f/Lap^f X Lap^s/Lap^s	14	38	22	19	39	15
A73-25050 X PI 407195 Zymogram type 1 X 2 Lap^f/Lap^f X Lap^s/Lap^s	13	15	6	24	55	21
Norredo X Lindarin Zymogram type 2 x 1 Lap^s/Lap^s X Lap^f/Lap^f	7	16	8	25	45	22
Total observed:	38	69	36	68	139	58
χ^2 (expected 1:2:1) =		0.23 = n.s.			1.40 = n.s.	

PI 407195 is a *G. soja* accession, while A73-25050 is an experimental *G. max* line.

Table 6. Inheritance of alleles at the soybean *Mpi* locus

Crosses	F_2 seeds and F_2* plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1	H	2	1	H	2
Mpi genotypes:	Mpi^f/Mpi^f	Mpi^f/Mpi^m	Mpi^m/Mpi^m	Mpi^f/Mpi^f	Mpi^f/Mpi^m	Mpi^m/Mpi^m
Chestnut X Amsoy Zymogram type 1 X 2 Mpi^f/Mpi^f X Mpi^m/Mpi^m	3	7	5	21	46	21
A73-25050 X PI 407195 Zymogram type 1 X 2 Mpi^f/Mpi^f X Mpi^m/Mpi^m	4	17	8	14	41	20
Hill X T145 Zymogram type 2 Mpi^m/Mpi^m X Mpi^f/Mpi^f	106	199	90			
Total observed:	113	223	103	35	87	41
χ^2 (expected 1:2:1) =		0.57 = n.s.			1.18 = n.s.	
Zymogram types:	1	H	3	1	H	3
Mpi genotypes:	Mpi^f/Mpi^f	Mpi^f/Mpi^s	Mpi^s/Mpi^s	Mpi^f/Mpi^f	Mpi^f/Mpi^s	Mpi^s/Mpi^s
Hark X PI's 65549 & 135624 Zymogram type 1 X 3 Mpi^f/Mpi^f X Mpi^s/Mpi^s	9	31	8	29	45	23
Total observed:	9	31	8	29	45	23
χ^2 (expected 1:2:1) =		4.37 = n.s.			1.24 = n.s.	
Zymogram types:	2	H	3	2	H	3
Mpi genotypes:	Mpi^m/Mpi^m	Mpi^m/Mpi^s	Mpi^s/Mpi^s	Mpi^m/Mpi^m	Mpi^m/Mpi^s	Mpi^s/Mpi^s
Cayuga X Evans Zymogram type 2 X 3 Mpi^m/Mpi^m X Mpi^s/Mpi^s	23	47	19	10	18	8
Amsoy X Wilson Zymogram type 2 X 3 Mpi^m/Mpi^m X Mpi^s/Mpi^s	29	40	21	22	39	17
Total observed:	52	87	40	32	57	25
χ^2 (expected 1:2:1) =		1.74 = n.s.			0.88 = n.s.	

PI's 65549, 135624, and 407195 are *G. soja* accessions, while A73-25050 and T145 are experimental *G. max* lines.

*F_2 plant progenies and F_2 seeds were the same except for those F_2 seeds which did not germinate, since the electrophoretic technique is nondestructive allowing progeny tests on the same F_2 seeds.

Table 7. Inheritance of alleles at the soybean *Pgd* locus

Crosses	F_2 seeds		F_2 plant progenies			F_3 seeds from segregating F_2 plants	
Zymogram types	1	3	1	Seg	3	1	3
Pgd genotypes:	$Pgd^f/-$	pgd/pgd	Pgd^f/Pgd^f	Pgd^f/pgd	pgd/pgd	$Pgd^f/-$	pgd/pgd
PI 406684 X A73-109084 Zymogram type 3 X 1 pgd/pgd X Pgd^f/Pgd^f	29	10	2	3	1	82	29
Hark X PI's 65549 & 135624 Zymogram type 1 X 3 Pgd^f/Pgd^f X pgd/pgd	42	12	2	3	2	96	32
Total observed:	71	22	4	6	3	178	61
χ^2 (3:1, 1:2:1, 3:1) =	0.09 = n.s.					0.04 = n.s.	

Crosses			
Zymogram types:	1	H	2
Pgd genotypes:	Pgd^f/Pgd^f	Pgd^f/Pgd^s	Pgd^s/Pgd^s
Hill X T145 Zymogram type 1 X 2 Pgd^f/Pgd^f X Pgd^s/Pgd^s	94	207	90
Agate X Elton Zymogram type 2 X 1 Pgd^s/Pgd^s X Pgd^f/Pgd^f	18	41	16
Total observed:	112	248	106
χ^2 (expected 1:2:1)		2.09 = n.s.	

PI's 406684, 65549 and 135624 are *G. soja* accessions, while A73-109084 and T145 are experimental *G. max* lines.

Seg equals segregating in the F_3 generation.

Table 8. Inheritance of alleles at the soybean *Pgi* locus

Crosses	F_2 seeds and F_2* plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1	H	3	1	H	3
Pgi	Pgi^f/Pgi^f	Pgi^f/Pgi^s	Pgi^s/Pgi^s	Pgi^f/Pgi^f	Pgi^f/Pgi^s	Pgi^s/Pgi^s
Hark X PI's 65549 & 135624 Zymogram type 1 X 3 Pgi^f/Pgi^f X Pgi^s/Pgi^s	14	31	13	39	62	37
PI 407302 X Beeson Zymogram type 3 X 1 Pgi^s/Pgi^s X Pgi^f/Pgi^f	4	19	7			
Total observed:	18	50	20	39	62	37
χ^2 (expected 1:2:1) =		1:73 = n.s.			1.48 = n.s.	

Table 9. Inheritance of alleles at the soybean Pgm_1 and Pgm_2 loci

Crosses	F_2 seeds and F_2* plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1,3	H	2,4	1,3	H	2,4
Pgm_1 genotypes:	$\frac{Pgm_1^f}{Pgm_1^f}$	$\frac{Pgm_1^f}{Pgm_1^s}$	$\frac{Pgm_1^s}{Pgm_1^s}$	$\frac{Pgm_1^f}{Pgm_1^f}$	$\frac{Pgm_1^f}{Pgm_1^s}$	$\frac{Pgm_1^s}{Pgm_1^s}$
Wells X PI's 423990A & 423988 Zymogram type 2 X 3 Pgm_1^s/Pgm_1^s X Pgm_1^f/Pgm_1^f	14	37	20	22	51	21
Chestnut X Amsoy Zymogram type 2 X 1 Pgm_1^s/Pgm_1^s X Pgm_1^f/Pgm_1^f	5	6	4	32	55	28
Hark X PI 65549 Zymogram type 1 X 2 Pgm_1^f/Pgm_1^f X Pgm_1^s/Pgm_1^s	8	15	10	14	26	11
Amsoy X Wilson Zymogram type 1 X 2 Pgm_1^f/Pgm_1^f X Pgm_1^s/Pgm_1^s	24	49	26	3	16	6

PI's 65549, 135624, 407302, 423990A, 423988 are *G. soja* accessions, while T145 is a *G. max* experimental line.

Table 9. *Continued*

Crosses	F_2 seeds and F_2* plant progenies			F_3 seeds from H-type F_2 plants		
Zymogram types:	1,3	H	2,4	1,3	H	2,4
Pgm_1 genotypes:	$\frac{Pgm_1^f}{Pgm_1^f}$	$\frac{Pgm_1^f}{Pgm_1^s}$	$\frac{Pgm_1^s}{Pgm_1^s}$	$\frac{Pgm_1^f}{Pgm_1^f}$	$\frac{Pgm_1^f}{Pgm_1^s}$	$\frac{Pgm_1^s}{Pgm_1^s}$
Hill X T145						
Zymogram type 1 X 2	60	148	78			
Pgm_1^f/Pgm_1^f X Pgm_1^s/Pgm_1^s						
Total observed:	111	255	138	71	148	66
χ^2 (expected 1:2:1) =		2.99 = n.s.			0.60 = n.s.	
Zymogram types:	1,2	H	3,4	1,2	H	3,4
Wells X PI's 423990 & 423988	22	43	18	48	69	32
Zymogram type 2 X 3						
Amsoy X PI423990A						
Zymogram type 1 X 3	8	21	12	8	21	9
PI406684 X A73-109084						
Zymogram type 4 X 1	10	22	6	18	36	22
Total observed:	40	86	36	74	126	63
χ^2 (expected 1:2:1) =		0.82 = n.s.			1.48 = n.s.	

PI's 423990A, 423988 and 406684 are *G. soja* accessions, while A73-109084 is a *G. max* experimental line.

*F_2 plant progenies and F_2 seeds were the same except for those F_2 seeds which did not germinate, since the electrophoretic technique is nondestructive allowing progeny tests on the same F_2 seeds.

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1) 2 Implications of seed set on ms_2 ms_2 male-sterile plants in Raleigh [1-3]

We conducted tests in the summers of 1981 and 1982 to determine seed set on the maturity group 3 cultivar 'Williams' and its ms_2 ms_2 male-sterile isoline. In these studies, Williams plants segregating for male sterility and the maturity group 5 cultivar, 'Forrest', were grown outdoors in pots at three isolated sites. We identified sterile and fertile plants immediately at flowering using standard pollen germination techniques. Seven pots of each genotype were then arranged in a randomized block design at each site. To maintain an adequate insect population for cross pollination, a honey bee hive was placed near each test. We included Forrest in the tests as an additional pollen source for the male-sterile Williams genotypes. Two tests were planted in May to simulate full-season growing conditions, while a third test was delayed until July to simulate double-cropped conditions.

Results: The ms_2 ms_2 genotype yields only about 8% less than its male-fertile isoline under early-planted conditions in Raleigh (Table 1). This result is quite surprising because the male-sterile Williams genotype sets seed poorly in the midwestern environment of its origin and in our own late-planted experiment (Table 1) (Bernard and Cremeens, 1975). We do not think that male sterility "broke down" in our full season tests because male-sterile plants kept in the greenhouse (insect free) set no seed whatever in the summers of 1981 and 1982. We suspect that favorable air temperature effects on flower morphology and honey bee activity can explain our high full-season seed set versus our poor late-planted results (Robacker et al., 1982). Temperatures were high and near normal for the full-season tests, while temperatures were unseasonably low during flowering in the late-planted test. As a result, flowers did not open as fully in the late-planted test as they did in the full-season tests. In addition, low temperatures reduced the total number of bee flights in the late-planted test (our bee flight observations were casual, however). Partially closed flowers and reduced bee activity then apparently limited pollination of the male-sterile genotypes in the late-planted test, while no such restriction occurred in the full-season test. Since it is thought that the ms_2 gene has no effect on female fertility, it seems reasonable that extensive pollination should increase seed set.

Implications: The seed set we observed on full-season ms_2 ms_2 Williams genotypes is much greater than we have ever seen on ms_1 ms_1 male-sterile genotypes. In fact, seed set may be high enough to obtain a useful measure of seed yield on a male-sterile genotype, although sampling variance tends to be greater for male-sterile plants.

The improved seed set on the ms_2 ms_2 male-sterile plant apparently offers new flexibility in designing recurrent selection breeding programs. For example, phenotypic recurrent mass selection for seed yield should be practical. To date, this method has been used only for the improvement of seed composition (where few seed are required) in soybeans. Another possibility with high seed set is that one could monitor seed yield as chemical

Table 1. Means for ms_2 male-sterile and male-fertile traits at Raleigh, NC

Experiment	Yield	Pods	Seed weight	Seed	Height	n
	g/plant	No./plant	per 100 seed	per pod	inches	
Over years - early planted[§]						
Ms_2 —[†]	40.8^{NS}	120*	13.7*	2.54*	40*	13
ms_2 ms_2	37.7	87	18.7	2.26	38	12
1981 - early planted						
Ms_2 —	44.3^{NS}	113*	16.2*	2.39*	38*	7
ms_2 ms_2	37.4	76	20.1	2.25	34	5
1982 - early planted						
Ms_2 —	37.6^{NS}	127^{NS}	10.7*	2.71*	43^{NS}	6
ms_2 ms_2	37.9	97	17.7	2.26	43	7
1982 - late planted						
Ms_2 —	24.8*	72*	14.2*	2.42*	32*	7
ms_2 ms_2	3.9	11	17.8	1.80	32	7
Sample variances[‡]						
Ms_2 —	60	405	2.55	.0123	4.3	
ms_2 ms_2	117	762	4.17	.0219	12.2	

*Fertile and sterile genotypes significantly different at 0.05 level.

[†] Ms_2 — = male fertile; ms_2 ms_2 = male sterile.

[‡] Includes only early planted tests. Pooled df are 10 and 11 for fertile and sterile genotypes, respectively.

[§] Year x fertility interaction detected for the traits seed weight and seed per pod.

or other seed traits are improved using mass selection. In this way, a detrimental or negative correlation between a chemical trait under selection and seed yield could be detected early on in a selection study. As a case in point, we detected a negative relationship between seed yield and oleic acid content of seed oil only after several cycles of mass selection, where the ms_1 gene had been employed for crossing purposes. The relationship would probably have been detected (and dealt with) much earlier if the ms_2 rather than the ms_1 gene had been used.

The high seed set on the ms_2 ms_2 sterile plant must surely offer other possibilities for adaptation of the ms_2 gene to recurrent selection. The final utility of the gene in our program depends on the repeatability of male-sterile yield levels over several full-season environments and in later maturing lines than Williams. We are optimistic at present that the gene will be useful.

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2) Seed set on *G. falcata* and a proposal to use ms_2 male sterility in its hybridization with *G. max*

Seed set: Limited seed supply has severely curtailed research on *G. falcata*. Seed supply is limited primarily because *G. falcata* sets few seed in the greenhouse, even though flower production is rather profuse. We noticed this past summer that seed set is quite high when we grow this species out-of-doors near a honeybee hive. At the present, we have recovered over 3000 seed from two plants through honeybee pollination of the accession PI 246591. Upon close examination of flower morphology, we found that the stigma protrudes beyond the anther heads, spatially separating the male and female flower parts. Thus, insect or some other physical activity is apparently required to transfer pollen from the anthers to the stigma. This information should prove useful in the future studies of *G. falcata*. We have no evidence that self-incompatibility is a factor in seed set at present, because an isolated individual *G. falcata* plant will set seed well in the presence of honeybees.

The requirement of insect pollination for seed set (at Raleigh) leads us to speculate that the species may be often cross-pollinated rather than self-pollinated in its natural habitat, the dry regions of Australia. In this respect, *G. falcata* may be unusual in the Glycine and Soja subgenera of *Glycine*; the other species appear to be primarily self-pollinating. The cross-pollinating nature of *G. falcata* suggests that hybrid vigor may be more substantial in this species than in *G. max*. Currently, there are too few accessions of *G. falcata* to test this last hypothesis properly. A last implication from our observations is that *G. max* may be more distant from

the *G. falcata* than from the other *Glycine glycine* species, in an evolutionary sense. Hybridization of the two species may be difficult as well.

Hybridization with *G. max*: Reported attempts to obtain viable hybrids between *G. falcata* and *G. max* have failed thus far. Hood and Allen (1980) obtained 52 F_1 pods from 461 artificial fertilizations, but no hybrid plants could be recovered. Similarly, Newell and Hymowitz (1982) obtained six possible hybrid pods, but no hybrid plants, from 253 manual attempts at cross-pollinations, indicating that development of interspecific hybrid plants may be difficult. Since parasexual techniques are not yet well-developed for the *Glycine* genus, successful hybridization of the two species may depend on the advance and refinement of embryo rescue techniques.

A prerequisite to the study and refinement of embryo rescue techniques is the generation of large numbers of interspecific embryos. Such embryos have been obtained (Hood and Allen, 1980) by artificial cross-pollination, but this method is both time-consuming and labor-intensive. Realizing that honeybees are attracted to both *G. max* and *G. falcata*, we propose the use of honeybees and the ms_2-conditioned male sterility in *G. max* to help generate large numbers of interspecific embryos. Our rather simple scheme should provide a continual supply of embryos for study from June through August (in our area) without the need for manual cross pollination.

The procedure is as follows: a) Grow *G. max* plants segregating for ms_2-conditioned male sterility in the greenhouse under insect-free conditions. Plant numbers should be high enough to insure recovery of at least 10 male-sterile plants.

b) At flowering, identify and destroy fertile *G. max* plants, retaining male-sterile plants for cross-pollination. Identification could be carried out first by "thumbnail" tests for pollen shedding, with any plant shedding pollen being discarded. Remaining plants could then be identified by pollen germination technique (Brim and Kenworthy, 1977), or simply by watching for pod formation (which usually is visible two weeks after flower initiation).

c) After male-sterile *G. max* plants have been identified with certainty, move the plants outside and surround with flowering plants of *G. falcata*. This crossing block should be kept well-isolated from other *Glycine* plants (Nelson and Bernard, 1979). Place an active honeybee hive near the crossing block.

d) Interspecific pollination should result in small pods on the male-sterile plants and can be used for embryo studies. Virtually no *G. max* embryos will develop in the crossing block. It should be noted, however, that male-sterile *G. max* plants form pod-like structures near the end of the flowering period, independent of fertilization. Practice is, therefore, needed to distinguish these "pseudo pods" from the pods of interest. Haploid seed may occasionally be produced on the sterile plants as well, but should not constitute a real concern.

e) The male-sterile plants will flower well for only about six weeks (under our conditions). Therefore, successive plants of *G. max* (possibly 2 or 3 weeks apart) are necessary to maintain receptive male-sterile plants. Late in the summer, photoperiod manipulation in a greenhouse may be required to obtain plants of adequate size. *G. falcata* should bloom continuously through the summer, but pods need to be picked and new plants added periodically in the crossing block to insure a profusion of flowers.

We tried the procedure on a limited basis this past fall, but little pollen was actually transferred. Cool air temperature reduced bee flights and caused the *G. max* flowers to remain partially closed. A favorable (i.e., summer) environment is, therefore, needed for the procedure to work.

As a final note, it may be necessary to double the chromosome number of *G. falcata* for successful hybridization with *G. max*. We do not know how such a change in chromosome number will affect pollen production and honeybee visitation.

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3) Inheritance of fatty acid composition in soybean seed oil

While it has been demonstrated that the fatty acid composition of soybean oil can be changed by recurrent selection (Wilson et al., 1981), there is little information about the genetic control of oil biosynthesis in soybean seeds. In some species, such as rape (Downey and Harvey, 1963), safflower (Yermanos et al., 1967), and flax (Yermanos and Knowles, 1962), the male parent has a significant effect on the fatty acid composition of oil from F_1 hybrid seeds. In corn (Jellum, 1966) and soybeans (Brim et al., 1968), the male parent has almost no effect on oil composition of F_1 hybrid seeds. In these two species, the hybrid seed has oil that is phenotypically similar to that of selfed seed from the maternal plant. The purpose of the experiment reported here was to study the inheritance of fatty acid components of seed oil and also re-examine the maternal influence on fatty acid composition of oil.

Materials and methods: In the summer 1981, reciprocal crosses were made between the PI, 'Peking', which has high percent 18:3 (linolenic acid), and N78-2245 (a breeding line we developed), which has low percent 18:3. Hybrid seeds were cut in half with a razor blade and were extracted in 3 ml of chloroform:hexane:methanol (2.0:1.25:0.5 v/v/v), filtered and dryed under N_2 gas. The extracts were taken up in 2:1 chloroform:methanol, filtered once more and analyzed by a Hewlett Packard 5880 gas chromatograph. The other half of each seed was planted in the greenhouse to determine which were actually

hybrids and which were selfs. Samples of F_2 seeds from mature F_1 plants were ground and oil was extracted as previously described (Wilson et al., 1981). F_2 soybean plants were grown to maturity in the field at Clayton, NC, in 1982. Single plants were harvested, and the fatty acid composition of the seed oil from each plant was determined.

Results and discussion: The fatty acid composition of oil from F_1 hybrid seeds showed a maternal influence similar to that described previously by Brim et al. (1968). The percentages of oleic (18:1), linoleic (18:2), and linolenic (18:3) acids of the hybrid seeds were not significantly different from those of self-pollinated seed from the maternal parent in either of the reciprocal crosses (data not shown). While the fatty acid composition of seed oil was maternally determined, it was not maternally inherited, because oil from seeds produced on F_1 plants had a fatty acid composition intermediate to Peking and N78-2245. In addition, the reciprocal crosses had nearly identical phenotypes (Table 1).

The results also suggested that dominance or epistasis effects were involved in determining fatty acid composition. In seed from the F_1 plants, the percentages of all fatty acid components except palmitic acid (16:0) were between those of the midparent and Peking in magnitude (Table 1). Thus, the Peking parent may have contributed dominant genes for low percentages of 18:1 and high percentages of 18:2 and 18:3, and/or epistatic gene interactions may have been responsible. The F_2 population of the crosses showed similar results with respect to 18:1 and 18:2 (Figure 1). Plants with seed oil percentages of 18:1 less than the F_2 population mean of 26.5 occurred in highest frequencies. Also, a majority of F_2 plants had percentages of 18:2 greater than the population mean of 50.4 (Figure 1). Percentages of 18:3 were more normally distributed (Figure 1) around the population mean of 8.1.

At this point, it is not clear which kinds of gene action are most important in the determination of fatty acid composition. Four cycles of recurrent mass selection for high 18:1 resulted in a linear increase in the percentage of 18:1 in seed oil (Wilson et al., 1981). This suggests that percent 18:1 is a typical quantitative genetic trait with additive gene effects involved in the phenotypic expression. The deviation of the F_1 from the midparent may indicate dominance, but the occurrence of dominance effects with quantitative traits is unusual in self-pollinated species. Epistasis is more likely to be involved in the deviation.

Current biochemical evidence indicates that the polyunsaturated fatty acids, 18:2 and 18:3, are produced by consecutive desaturation of 18:1 (Cherif et al., 1975). A possible biochemical explanation of the data would postulate a dual-enzyme desaturase complex to perform the two reactions.

$$18{:}1 \xrightarrow[1]{\text{NADH} \curvearrowright \text{NAD}} 18{:}2 \xrightarrow[2]{\text{NADH} \curvearrowright \text{NAD}} 18{:}3$$

The amount of the total enzyme complex would regulate the relative percentages of 18:1 and 18:2. More enzyme would result in more 18:1 desaturation and hence more 18:2 production. According to this hypothesis, N78-2245 and Peking would supposedly have small and large amounts, respectively, of the enzyme complex. The total amount of the complex and the amount of 18:1 formed could be controlled by several additive genes.

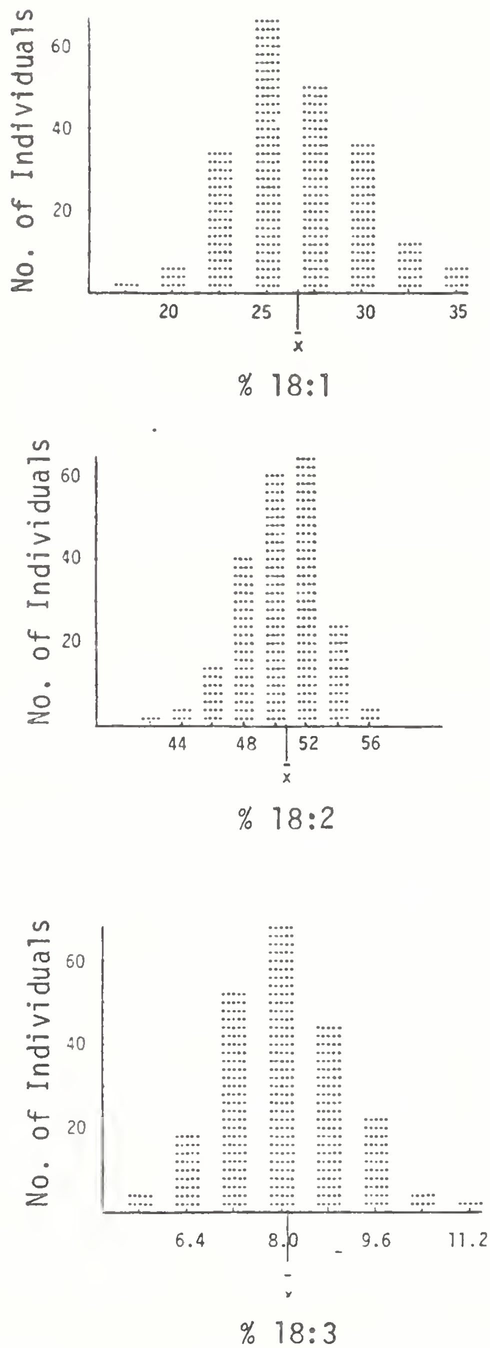

Figure 1. Distributions with respect to fatty acid components of seed oil from field-grown F_2 plants of the cross Peking x N78-2245.

Table 1. Mean fatty acid composition of seed oil from greenhouse-grown F_1 soybean plants and parents of the cross Peking x N78-2245

Material	Fatty Acid				
	16:0	18:0	18:1	18:2	18:3
			mole %		
Peking	11.7	3.3	19.9	54.5	10.6
Peking[a] x N78-2245 F_1 plants	11.5	3.8	23.3	52.9	8.5
N78-2245[a] x Peking F_1 plants	11.5	3.9	22.2	53.7	8.7
N78-2245	9.6	4.0	46.8	34.7	4.9
Midparent	10.6	3.7	33.3	44.6	7.8

[a]Maternal parent.

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4) Influence of maturity date on the oil content of soybeans with genetically altered fatty acid composition.

Recurrent mass selection and within half-sib family selection for increased oleic acid percentage has been proven successful in decreasing the percentage of linolenic acid in soybean oil (Burton et al., 1983). In the first four cycles of selection, the percentage of oleic acid in the seed oil increased linearly at an average rate of 1.6 $\pm$ 0.2% per cycle whereas linoleic and linolenic acid percentages showed linear decreases. Four additional cycles of selection for increased oleic acid and two cycles for decreased oleic acid levels are currently being evaluated in a wide range of environments. From that investigation, it has become increasingly evident that the number of maturity days from planting has decreased with selection. A shift in maturity date in the selected populations may warrant modification of existing selection procedures if maturity effects are confounded with the effects of genes that directly control the fatty acid composition of oil. The results reported here suggest that the fatty acid composition of soybean oil may be influenced by the period of time during the growing season when the plants mature.

A segregating F_4 population of 182 plants from a cross between 'Tracy' and N79-2002, an experimental line selected from the sixth cycle of mass selection, was grown in Clayton, NC, in 1982. Date of maturity was monitored on a weekly basis, and seed from single plants were analyzed for fatty acid composition at harvest maturity. Average percentages of unsaturated fatty acids of F_4 lines within a maturity date set were reported in Table 1. Because each set represented a random sample of lines with respect to fatty acid composition, the means should not have differed among sets beyond that expected due to sampling. Therefore, a shift in the percentages of unsaturated fatty acids would be a result due to maturity date differences if there were no linkages between genes controlling maturity and genes controlling fatty acid composition. Although there was very little change in the proportions of fatty acids among the final three maturity dates, the percentage of oleic acid decreased while the percentages of the polyunsaturated fatty acids, linoleic and linolenic acids, generally increased from September 17 to October 5. There was no consistent trend observed for the levels of palmitic and stearic acids and, thus, were not reported.

The same trends were found in another experiment in which N78-2245 was planted on three dates (May 5, June 6, and June 28, 1982) in two replications to induce a wide range of maturity dates (Table 2). N78-2245, a highly inbred experimental line, was selected on the basis of high oleic acid concentration from the fifth cycle of mass selection, followed by within half-sib family selection. Over a period of 29 days, the mean percentage of oleic acid in N78-2245 decreased by 9.2 mole% while the mean percentages of linoleic and linolenic acids increased by 6.6 and 0.9 mole%. In addition, the proportion of shriveled seeds declined dramatically over maturity dates. Probably as a result of insufficient replication, the effect of maturity date on fatty acid percentage was not statistically significant at the 5% level. The noted trends in unsaturated fatty acid composition, however, predicate a source of concern for the genetic improvement of a trait so highly influenced by environmental factors.

Previous reports have suggested that seed maturation under a warmer environment, i.e., as a result of earlier planting, may result in lower percentages of the polyunsaturated fatty acids (Howell and Collins, 1957; Unger and Thompson, 1982). From another viewpoint, the lower levels of polyunsaturated fatty acids observed at the early maturity date may have resulted from a shortened pod-filling period, as indicated by the higher proportion of shriveled seeds. In that regard, the deposition of polyunsaturated fatty acids in N78-2245 seed oil predominates late in seed development (Carver et al., n.d.). In concluding, it may prove beneficial to consider maturity date in addition to oleic acid percentage when trying to reduce linolenic acid content in a soybean population.

Table 1. Unsaturated fatty acid composition of an F_4 population from the cross Tracy x N79-2002

Maturity date	No. of plants analyzed	Oleic acid	Linoleic acid	Linolenic acid
			%[a]	
September 17	21	38.1 ± 1.1	41.3 ± 0.9	5.8 ± 0.1
September 24	35	37.0 ± 1.3	42.9 ± 1.0	5.9 ± 0.2
September 30	34	36.2 ± 1.3	42.6 ± 1.0	6.2 ± 0.1
October 5	53	35.9 ± 0.8	43.0 ± 0.6	6.6 ± 0.1
October 12	29	36.1 ± 1.0	43.0 ± 0.8	6.4 ± 0.2
October 18	10	36.2 ± 1.6	43.0 ± 1.3	6.3 ± 0.2

[a]Means and standard error of single plant analyses within a maturity date set.

Table 2. Effect of maturity date on the unsaturated fatty acid composition of N78-2245

Maturity date	% Shriveling	Oleic acid	Linoleic acid	Linolenic acid
			mole%[a]	
September 10	78	49.5	33.2	4.5
September 28	37	46.9	35.5	4.5
October 8	20	40.3	39.8	5.4
$S_{\bar{x}}$	7	4.2	3.4	0.4

[a]Each analysis = 6 samples from each of 2 reps.

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1) 147 Midwest soybean rhizobotanical survey [ ].

Plant root systems have a characteristic morphology that is modified by the edaphic conditions in which they grow. Soil texture, moisture, temperature, and depth of penetrable soil all modify root morphology. Genetic characteristics of the plant control the basic root morphological characteristics. In addition, cultural practices - tillage, row spacing, fertilization, pesticide/herbicide applications - also have an effect on root morphological development.

It is unclear what the relative importance of these differing components of the biology of a plant have on the development of a plant root system. In an attempt to get a handle on this problem, [six cultivars with known root characteristics ~~were~~ grown in 7 states during the 1981 growing season]. Nine different rooting characteristics, including four nodulation characteristics and three shoot characteristics, were scored. The 12 tables below show the mean value of each character in each cultivar at each midwest location plus California (a total of six locations).

Experimental plots were of randomized complete block design with four replicates (three in Indiana). Samples consisted of three plants per replicate per cultivar; therefore, at a location, cultivar means were derived from a total of twelve plants. Sampling consisted of the plant root system excavated by a single spade full of soil. The sampling period for the Midwest sites was from the last week in July to the first week in August. Locations were sampled in the numerical order presented. The California plot was sampled on August 12. There was no attempt to standardize agronomic practices. This may represent the basis for much of the site-by-site variability.

Table 13 presents the levels of significance for analyses of variance carried out on the data for the previous 12 tables. The environment has a significant effect on every character, while there are no significant cultivar differences for number of nodules on the tap root, or number of collateral roots. The environment-genotype interaction is significant at the 1.0% level for numbers of medium and large nodules, nodule diameter, and basal root diameter; and highly significant (0.01%) for the three shoot characteristics: hypocotyl diameter, plant height, and developmental stage.

This preliminary study indicates that all root characteristics are environmentally sensitive; witness the significant response of each character to the six differential environments. However, some of the characters are conditioned by genes whose alleles (represented by different cultivars) do not appear to be differentially sensitive to the environment. This is best demonstrated by the lack of an interaction between cultivars and environment for tap root diameter at the 6-centimeter level even though there is significant genotypic and environmental variance. Those characteristics that strongly interact with the environment, e.g., developmental stage, may not be fully predictable across environments. A single-year experiment cannot reliably point to specific factors and causes, but it can be used for an initial analysis of the interdependence of the two sources of variability: genotype vs. environment. Further studies along these lines should develop some very interesting results.

The following tables use this identification code: FIELD: 1 = Wooster, OH; 2 = West Lafayette, IN; 3 = Urbana, IL; 4 = Ames, IA; 5 = Lincoln, NB; 6 - Davis, CA. Plots were usually at research stations which, in several cases, were a considerable distance away from the indicated cities. CULTIVAR: 1 = Chippewa 64; 2 = Rampage; 3 = Harosoy 63; 4 = Corsoy 71; 5 = Wells; 6 = SRF 150P.

Table 1. Number of nodules on the tap root

	Field						
Cultivar	1	2	3	4	5	6	M
1	0.58	10.44	21.58	21.08	3.75	11.75	11.58
2	0.92	6.78	17.92	19.42	5.58	15.00	11.12
3	1.17	7.62	16.42	21.33	7.50	13.08	11.35
4	0.67	9.56	14.92	23.17	8.67	15.42	12.17
5	1.08	13.67	23.50	20.25	7.67	---	13.21
6	0.75	8.67	20.00	16.25	7.08	10.00	10.54
M	0.86	9.46	19.06	20.25	6.71	13.05	11.61

Table 2. Number of large and medium size nodules on the rest of the root system

	Field						
Cultivar	1	2	3	4	5	6	M
1	1.42	15.67	9.83	36.00	2.83	16.67	13.65
2	3.17	16.00	24.58	60.58	2.25	18.33	21.03
3	6.25	10.67	27.42	62.75	6.25	16.17	22.06
4	4.92	19.22	35.67	71.42	10.42	23.58	27.90
5	3.33	11.56	26.58	42.08	11.75	---	19.46
6	3.50	14.33	46.92	54.83	11.67	22.58	26.13
M	3.76	14.57	28.50	54.61	7.53	19.47	21.77

Table 3. Number of small nodules on the rest of the root system

	Field						
Cultivar	1	2	3	4	5	6	M
1	0.08	5.33	5.75	4.42	3.67	2.75	3.59
2	0.00	4.89	20.67	6.17	5.92	5.08	7.22
3	0.08	4.22	15.83	6.42	21.25	10.08	9.88
4	0.00	4.89	19.82	10.25	11.25	15.50	10.54
5	0.17	5.44	7.17	5.00	16.75	---	6.89
6	0.17	3.33	16.08	8.67	18.00	12.92	10.14
M	0.08	4.68	14.24	6.82	12.80	9.27	8.09

Table 4. Number of basal roots

Cultivar	Field 1	2	3	4	5	6	M
1	5.33	4.22	2.25	4.42	4.08	5.00	4.22
2	5.67	2.89	3.41	4.75	3.25	5.08	4.23
3	6.42	3.00	3.25	7.83	3.67	5.08	4.96
4	6.00	4.22	4.50	5.08	1.83	4.25	4.32
5	7.83	5.78	4.75	7.83	5.08	--	6.28
6	6.08	4.44	6.08	4.83	4.42	4.17	5.03
M	6.22	4.09	4.04	5.79	3.72	4.72	4.80

Table 5. Number of lateral roots

Cultivar	Field 1	2	3	4	5	6	M
1	6.83	7.11	6.17	12.92	12.67	10.00	9.38
2	6.25	8.11	7.17	11.33	15.33	9.42	9.67
3	10.42	7.00	10.00	16.67	17.75	10.58	12.29
4	10.67	9.11	11.33	17.17	16.67	9.75	12.59
5	12.00	11.00	10.58	13.58	11.91	---	11.86
6	7.83	7.33	8.25	13.75	12.75	10.08	10.12
M	9.00	8.28	8.92	14.24	14.51	9.97	10.96

Table 6. Number of collateral roots

Cultivar	Field 1	2	3	4	5	6	M
1	25.00	28.56	29.08	27.08	21.67	28.83	26.62
2	27.08	27.11	30.33	25.75	21.17	31.25	27.12
3	24.25	27.44	35.25	33.33	19.58	41.42	30.33
4	20.50	29.33	35.08	25.08	23.00	36.83	28.26
5	17.50	31.33	28.25	32.17	20.00	---	25.56
6	24.00	26.67	25.92	28.67	20.75	36.00	27.01
M	23.06	28.41	30.65	28.68	21.03	34.87	27.54

Table 7. Nodule diameter (mm)

	Field						
Cultivar	1	2	3	4	5	6	M
1	2.75	3.01	3.38	3.66	1.29	4.25	3.06
2	2.72	2.71	3.42	3.49	1.59	4.08	3.02
3	4.76	2.63	3.15	3.19	1.43	3.99	3.22
4	3.68	2.86	3.32	3.32	1.80	4.12	3.20
5	4.53	3.58	3.67	3.84	1.89	--	3.50
6	2.95	2.80	3.05	3.46	1.42	4.16	2.98
M	3.57	2.93	3.33	3.49	1.57	4.12	3.15

Table 8. Basal root diameter at the base

	Field						
Cultivar	1	2	3	4	5	6	M
1	2.07	2.23	1.48	1.73	3.10	2.94	2.26
2	2.68	1.78	2.74	2.04	2.70	2.92	2.51
3	2.09	2.12	1.98	1.26	2.93	2.47	2.14
4	1.80	1.85	1.87	1.04	1.39	2.83	1.79
5	3.18	3.13	3.62	2.38	3.31	--	3.12
6	2.26	2.27	3.06	1.41	2.39	2.36	2.29
M	2.34	2.23	2.46	1.64	2.64	2.70	2.33

Table 9. Tap root diameter six centimeters below its base

	Field						
Cultivar	1	2	3	4	5	6	M
1	2.18	2.67	2.87	1.73	1.76	2.57	2.28
2	2.42	2.24	2.60	1.79	1.96	2.40	2.24
3	1.76	1.88	2.09	1.52	1.82	2.57	1.94
4	1.80	1.67	2.09	1.37	1.58	2.21	1.79
5	2.63	3.03	2.88	2.56	2.17	--	2.64
6	1.88	2.09	2.75	1.48	1.93	2.63	2.13
M	2.11	2.26	2.55	1.74	1.87	2.48	2.15

Table 10. Hypocotyl diameter at the cotyledons

	Field						
Cultivar	1	2	3	4	5	6	M
1	5.83	5.78	5.60	6.50	7.92	8.25	6.85
2	6.12	5.94	6.96	6.42	6.50	7.67	6.63
3	5.84	5.33	5.36	6.33	6.96	6.52	6.09
4	5.87	5.66	6.12	6.33	5.92	7.21	6.21
5	8.50	7.78	8.62	7.83	9.14	--	8.41
6	5.97	5.33	9.17	6.25	6.33	7.62	6.84
M	6.35	5.97	6.97	6.11	7.13	7.45	6.76

Table 11. Plant height (cm)

	Field						
Cultivar	1	2	3	4	5	6	M
1	63.58	62.06	88.35	100.67	84.17	85.29	81.50
2	56.80	52.72	73.96	94.81	73.58	85.83	73.83
3	73.13	70.80	92.39	118.08	97.33	104.83	93.72
4	70.88	68.38	90.21	122.50	98.46	103.42	93.35
5	50.22	50.13	85.44	97.85	80.21	---	73.96
6	51.40	55.67	95.14	109.71	90.29	91.42	83.43
M	61.00	59.96	87.58	107.27	87.34	94.16	83.58

Table 12. Developmental stage

	Field						
Cultivar	1	2	3	4	5	6	M
1	3.00	2.33	2.75	3.67	3.50	2.00	2.90
2	2.92	2.00	2.50	3.33	2.58	2.00	2.58
3	2.67	2.00	1.83	3.08	2.83	2.00	2.42
4	2.33	2.00	2.25	2.83	3.08	2.00	2.43
5	2.00	1.56	2.42	2.83	2.50	--	2.30
6	2.42	2.00	3.25	3.08	2.50	2.00	2.56
M	2.55	1.98	2.50	3.14	2.83	2.00	2.54

Table 13. Probability that a sample with a higher variance would be found through random sampling (from a two-way analysis of variance)

Character	Cultivar variance	Location variance	Interaction (C x L)
Nodule no.			
on the tap root	NS	0.01%	NS
Large/medium	0.01%	0.01%	1.0%
Small	1.0%	0.01%	NS
Root no.			
Basal	0.1%	0.01%	NS
Lateral	0.04%	0.01%	NS
Collateral	NS	0.01%	NS
Diameters			
Nodule	0.1%	0.01%	1.0%
Basal	0.01%	0.01%	1.0%
Tap - 6 cm	0.01%	0.01%	NS
Hypocotyl	0.01%	0.01%	0.01%
Plant height	0.01%	0.01%	0.01%
Developmental stage	0.01%	0.01%	0.01%

The following individuals were instrumental in carrying out these experiments: Drs. Richard Cooper, Stan Barber, Doyle Peters, Tom Kaspar, Jerry Eastin and Don Phillips.

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1) 245 A new gene for peanut mottle virus resistance in soybean.

Boerma and Kuhn (1976) established that 'Dorman' and 'CNS' each contain a single dominant gene conditioning resistance to peanut mottle virus (PMV). The gene was labelled *Rpv*, but it was not demonstrated that the genes in the cultivars were allelic. Shipe et al. (1979) also demonstrated the presence of single dominant genes for PMV resistance in each of 'Arksoy', 'PI 89784' and 'PI 219789', but made no tests for allelic relationships. Other dominant sources of resistance to PMV include the cultivars 'York' (Roane and Tolin, 1974) and 'Shore' (unpublished data). Shipe et al. (1979) also have reported a recessive gene for PMV resistance in 'Peking'.

Based on pedigree analysis, Shipe (1978) assumed that the gene for resistance in York was derived from Arksoy via Dorman. He also had evidence that Arksoy and CNS carried different genes for resistance.

This study was undertaken to elucidate the relationships among genes conditioning PMV resistance from three closely related sources (York, Dorman and Arksoy) and two relatively unrelated sources (CNS and Shore).

Crosses were made among plants of each parent that was proven to be PMV resistant. F_1 plants from eight of the ten possible crosses were grown in the field or greenhouse. F_2 plants of each cross were grown at the Eastern Virginia Research Station, Warsaw, and harvested individually. In 1982, F_3-progeny rows were planted at Blacksburg and at about three weeks of age were inoculated with PMV using an artist's air brush. Approximately 50 seed from about 100 F_2 plants of each cross were planted along with 'Lee 68' as a susceptible check.

Counts of susceptible and total plants were obtained for each row about four weeks after inoculation. A large number of rows had only one or two susceptible plants. Since we needed to distinguish completely resistant rows from those segregating 15 resistant:1 susceptible, most plants with symptoms in rows with one or two symptomatic plants were sampled for an ELISA test (Clark and Adams, 1977). If no plants in a row were positive for PMV, the whole row was classified as resistant.

If both parents of a resistant x resistant cross carry the same gene, all progeny should be totally resistant. If the parents contain genes at different loci, the progenies of F_2 plants can exhibit four different segregation ratios. The four classes and expected frequencies are: all resistant (7/16), 15 resistant:1 susceptible (4/16), 3 resistant:1 susceptible (4/16), and all susceptible (1/16).

Data from all segregating rows were subjected to a χ^2 test for both a 15:1 and a 3:1 ratio and assigned to the class for which the probability was highest. These data were then tested against the 7:4:4:1 F_2 ratio.

Table 1 summarizes the results from all crosses among York, Shore, Arksoy and Dorman. It appears that there is no segregation for PMV reaction, since no rows were all susceptible or segregated 3 resistant:1 susceptible. A few plants gave a positive test for PMV, but we do not believe these plants

represent genetic segregation. Rather, it appears that they were exhibiting a hypersensitive reaction. Seeds were harvested from most of these plants and we are currently testing that theory. Inoculations appeared to be very successful since the Lee 68 rows were nearly 100% infected throughout the nursery.

Table 1. Summary of field reactions of F_3 lines from four crosses of soybeans to inoculation with PMV and ELISA results

	No. of F_3 rows		No. plants		
				ELISA	
Cross	Total	With "S" plants	Total "S"	PMV pos.	PMV neg.
York x Shore	100	30	33	1	32
Dorman x Shore	100	32	45	10	29
Arksoy x York	97	60	120	13	107
Arksoy x Dorman	50	33	50	4	45
Dorman x Arksoy	50	25	42	2	32
Dorman x York	69	25	41	16	15

Table 2 summarizes the results of all crosses with CNS. All three crosses provide a good fit to the 7:4:4:1 ratio expected when different genes are present in the parents. While the combined data do not provide a good fit to the ratio, they are very homogeneous. It appears that the poor overall fit is due largely to the misclassification problems indicated earlier. The greatest imbalance is in the 15:1 class of which there was an excess, while the all-resistant class had a deficiency. Just a very few misclassified plants in genetically resistant rows could account for this imbalance.

Table 2. Reactions to field inoculation with PMV of F_3 families from crosses with CNS

	No. of families				χ^2	
		Segregating				
Cross	all R	15R:1S	3R:1S	all S	7:4:4:1	P
Dorman x CNS	37	29	23	11	4.429	.2-.3
Shore x CNS	40	31	20	9	3.971	.2-.3
York x CNS	39	35	23	7	4.429	.2-.3
TOTALS	116	95	66	27	12.829 (9df)	
				Pooled	11.607 (3df)	< .01
				Heterogeneity	1.222 (6df)	.95-.98

In summary, the available data support the conclusion that York, Shore, Arksoy and Dorman contain the same gene for resistance to PMV but the dominant gene for resistance in CNS is at an independent locus. Assignment of a gene symbol will be done in a later manuscript when further details on the classification of some plants are obtained.

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2) Inheritance of a male-sterile mutant from irradiated Essex soybeans.

In 1976, a plant was selected from the M_3 generation of some 'Essex' soybeans that had been irradiated with neutrons and grown at the Eastern Virginia Research Station, Warsaw. The plant had a green stem and reduced seed set. The progeny row grown the following year had all normal appearing plants. A short progeny row was grown in 1978 from bulked seed of the previous year. Twenty of those plants appeared normal; 12 were typical of male-sterile plants. This ratio of fertile-to-sterile plants is an acceptable fit to a 3:1 ratio (P = .10). Progeny from each of the fertile plants were grown in the greenhouse to observe segregation for sterility. The results (Table 1) indicated that the trait was simply inherited, since the segregating progenies fit a 3:1 ratio very well and the ratio of segregating to non-segregating progenies provided a good fit to the expected.

Four independently inherited, recessive genes controlling male sterility in soybeans have been reported (Brim and Young, 1971; Bernard and Cremeens, 1975; Delannay and Palmer, 1982; Palmer et al., 1980) and identified as ms_1 through ms_4. Stocks of each were obtained and crossed with the Essex male sterile for allelism tests.

Table 1. Observed segregation of Essex male sterile soybean

Type of progeny	No. of families	Fertile	Sterile	df	3:1 χ^2	P
Segregating	15	187	57	15	14.738	
		Pooled data		1	.350	.55
		Heterogeneity		14	14.388	.42
All fertile	5	---	--	--	---	
χ^2 (2:1)*	.627 (P=.43)					

*Ratio based on assumption that all plants in original progeny row (1977) were heterozygous.

Results of crosses with L74-03 (ms_1) are shown in Table 2. Crosses were made between heterozygous plants of both stocks. All 11 F_1 plants were fertile, indicating that the genes were at different loci. In the F_2, half the families should segregate 3 fertile:1 sterile, one-fourth should segregate 9 fertile:7 sterile and one-fourth should be all fertile, if the two stocks have different genes. If the genes are allelic, two-thirds of the progenies of fertile F_1s should segregate 3 fertile to 1 sterile and one-third should be all fertile. No progenies were found to be all fertile, but since only 3 or 4 would be expected for either model, this should not invalidate either one. As shown in Table 2, the data provide the best fit to the two-gene model. All progenies were large enough to provide a good fit to only one of the possible ratios. The presence of families that clearly did not fit the 3:1 ratio, but did fit the 9:7 is positive evidence that two genes for male sterility were present.

Table 2. Segregation of F_2 families from crosses of heterozygous Essex male sterile soybean plants x *Ms_1 ms_1* plants

	Segregation ratio									
	3:1					9:7				
	No. plants fert.	No. plants ster.	df	χ^2	P	No. plants fert.	No. plants ster.	df	χ^2	P
Pooled	1123	412	1	2.773	.10	474	380	1	0.193	.34
Heterogeneity			6	4.778	.57			3	4.365	.22
Total			7	7.551				4	4.558	

Allelism tests with ms_2 were done somewhat differently. The Essex male-sterile stocks were planted in alternate rows in an isolated nursery with seeds from the genotype *cyt-G* y_3 Ms_2 ms_2 which had been developed by selecting male-sterile, yellow-seeded plants from advanced generations of hand pollination of L64-2584 (*cyt-G* y_3) with pollen from F_2 plants of L74-01 (ms_2) x V68-920 (normal fertility). Seeds were saved from all the male-sterile plants in the *cyt-G* y_3 ms_2 rows. All green seeds were assumed to be crosses to Y_3 plants (primarily the Essex male-sterile; a few green-seeded plants were found in the ms_2 rows, but crosses with them were eliminated later on the basis of nonsegregation for pubescence color, since all ms_2 plants were tawny and the Essex male-sterile was gray).

All the green seeds produced on the ms_2 plants were planted in the greenhouse and 44 plants were obtained. Of those, 10 were sterile and produced no seeds. Since intercrosses with the Y_3 plants in the ms_2 rows could not be ruled out, the presence of sterile plants was not a positive indicator of allelism between ms_2 and the Essex male sterile. The progenies of the fertile greenhouse plants were planted in the field and observed for male sterility. Thirteen of them had all tawny plants so were discarded as being intercrosses within the rows containing the ms_2 plants. The segregation of each of them fit a 3:1 ratio. The segregations of the remaining rows are summarized in Table 3. Although population sizes were rather small, there were several families that did not fit a 3:1 segregation, but provided a good fit to a 9:7. Also, the ratio of 3:1 to 9:7 families is an acceptable fit to the expected 1:1 (P = .13). A χ^2 test using all segregating progenies gives an overall poor fit to a 3:1 ratio (P = .02) and shows that they are not homogeneous (P <.001). Thus, the available evidence indicates that the Essex male sterile is not allelic to ms_2.

Crosses to test for allelism with ms_3 and ms_4 were made using T273H and T274H as the sources and using only male-sterile plants for maternal parents and heterozygous plants as pollen parents. Summaries of observed segregations in F_2 progenies are given in Tables 4 and 5 and conclusively show that the Essex male-sterile is not allelic to either ms_3 or ms_4. Each family was classified as segregating either 3:1 or 9:7 based on χ^2 tests. All of the families except six could be assigned on the basis of an acceptable fit (P <.05) to one ratio compared to an unacceptable fit to the alternate ratio. The heterogeneity χ^2 for the 3:1 families in Table 5 is rather high, but a large portion of that was due to one family in which a deficiency of male-sterile plants occurred.

Table 3. Segregation of F_2 families from crosses of ms_2 ms_2 soybean plants x heterozygous plants of Essex male sterile

	Segregation ratio									
	3:1					9:7				
	No. plants fert.	No. plants ster.	df	χ^2	P	No. plants fert.	No. plants ster.	df	χ^2	P
Pooled	261	71	1	2.313	.13	122	88	1	0.291	.59
Heterogeneity			13	9.994	.69			6	6.190	.40
Total			14	12.307				7	6.481	

Table 4. Segregation of F_2 families from crosses of male-sterile soybean plants of Essex male sterile x *Ms_3 ms_3* plants

	Segregation ratio 3:1					9:7				
	No. plants fert.	ster.	df	χ^2	P	No. plants fert.	ster.	df	χ^2	P
Pooled	1001	343	1	0.194	.66	497	354	1	1.601	.21
Heterogeneity			17	22.921	.15			10	7.123	.71
Total			18	23.115				11	8.724	

Table 5. Segregation of F_2 families from crosses of *ms_4 ms_4* soybean plants x heterozygous plants of Essex male sterile

	Segregation ratio 3:1					9:7				
	No. plants fert.	ster.	df	χ^2	P	No. plants fert.	ster.	df	χ^2	P
Pooled	305	92	1	0.706	.40	351	264	1	0.169	.68
Heterogeneity			4	10.873	.03			7	7.805	.35
Total			5	11.579				8	7.974	

The Essex male sterile is most like the *ms_1* male sterile in that plants typically produce only a few, one-seeded pods. It also might have a degree of female sterility, since it was difficult to obtain crosses on male-sterile plants. That was the reason for using heterozygous maternal parents in the *ms_1* crosses. Anthers of male sterile plants appear dark and shrunken and pollen grains appear small and shriveled under the microscope. Plants could be classified readily as fertile or sterile, based on the appearance of anthers and pollen.

In summary, the available data indicate that the Essex male sterile is not allelic to *ms_1*, *ms_2*, *ms_3*, or *ms_4*. Thus, it is proposed that the gene symbol *ms_5* be assigned to this mutant. It has been entered in the Genetic Type Collection as T277, and described as a semi-sterile until the mechanism of the sterility is studied further.

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1) The T270H chlorotic mutant: Inheritance and linkage analysis.

An unusual chlorotic mutant that is variably viable was found in 1977. Preliminary inheritance data and phenotypes of the mutant were described by Stelly, Muir and Palmer in 1979. Combined F_2 plant and F_3 family analyses suggested monogenic recessive inheritance of the chlorotic phenotype. Certain environments, particularly greenhouse environments, seemed to favor viability and nonchlorosis of homozygous mutant genotypes. We report herein results of inheritance and linkage tests of this mutant with K_1, W_1, and T_1.

F_2 and some F_3 plants were classified as green (Y -) or chlorotic ($y\ y$) and/or for flower color (W_1), saddle pattern (k_1) and pubescence color (T_1). F_3 families for F_2 Y - plants were classified as nonsegregating or segregating, corresponding to inferred genotypes of F_2 parents; e.g., $Y\ Y$ and $Y\ y$, respectively. Overall, plant and family segregation data support the conclusion that a recessive allele determines the chlorotic phenotype (Table 1). Heterogeneity among population-year combinations was evident, however, particularly between 1978 and 1981 - $W_1\ K_1\ Y$ populations, wherein significant deficiencies and excesses of chlorotic mutants were observed, respectively. Homogeneity for plant segregations among families within year-populations, however, was acceptable; e.g., 1981 - $W_1\ K_1\ Y$ population heterogeneity χ^2 = 17.88, 15 df (p = 0.25 - 0.50), when expected segregations were adjusted for overall segregation. Effects of environment and perhaps other factors (e.g., background genotype) may have added variation to plant-plant classification data.

Data from classifications of F_3 families for nonsegregation:segregation strongly supported the hypothesis of monogenic recessive inheritance, especially in that the data were very homogeneous across year-population combinations (Table 1, combined 3, 6, 7). Family classifications, of course, are much less subject to error resulting from environmentally induced miscalculations.

Two-factor linkage tests of 1981 $W_1\ T_1\ Y$ and 1982 $W_1\ K_1\ Y$ populations (data in Table 2) were made to detect nonindependent assortment of Y-K_1, Y-W_1, K_1-W_1, Y-T_1 and W_1-T_1 loci. In essence, two tests were made for linkage between the Y locus and K_1, W_1, and T_1 loci, and between W_1 and K_1 loci. Each test of monogenic ratios (Table 3) of K_1, W_1, and T_1 loci is confounded with a test of linkage, since selective recovery of alleles would accompany selection of the immediate Y- parent if loci were linked. For example, self-seed from only K_1-Y - F_2 plants were used for F_3 family analysis. Selection of Y - F_2-plant self-progeny for F_3 family analysis, of course, would have constituted inadvertent selection of a k_1 allele if k_1 and Y were linked (repulsion). Deviation from 3:1, i.e., excess $k_1\ k_1$, would have indicated linkage between Y and K_1 loci.

Table 1. Genotypic classification data and χ^2 tests for a chlorotic mutant in soybean

No.	Year	Population	Unit of classification	Observed incidence Y –:$y\,y$	Observed incidence $Y\,Y$:$Y\,y$	Ratio tested	χ^2 (Probability)	Homogeneity χ^2, df (Probability)
1.	1977	F_2†	Plant	92:34		3:1	0.27(0.5-0.7)	-
2.	1978	F_3	Plant	1118:327		3:1	4.33(0.025-0.05)	34.3305, 36 df (0.5-0.75)†††
3.	1978	F_3††	Family		11:37	1:2	2.34(0.1-0.25)	-
4.	1980	F_2	Plant	179:59		3:1	0.01(0.9-1.0)	0.13, 1 df (0.9-1.0)
5.	1981	F_2	Plant	1213:472		3:1	8.15(0.0-0.05)	17.88, 15 df (0.25-0.5)†††
6.	1981	F_2††	Family		55:120	1:2	0.29(0.5-0.75)	-
7.	1982	F_3††††	Family		201:399	1:2	0.01(0.9-1.0)	-
Combined 1, 2, 4, 5			Plant	2602:892			0.52(0.25-0.5)	71.35, 55 df (0.05-0.1)
Combined 3, 6, 7			Family		267:556		0.294(0.5-0.75)	2.34, 2 df (0.25-0.5)

† Mutant originally detected in this family.

†† F_3 family analysis of F_2 *Y*-plants.

††† Adjusted for overall *Y*-*y* distribution.

†††† F_3 family analysis of F_2 Y-k_1-plants.

Table 2. Genotypes of F_2 plants (1981 W_1 K_1 Y plant analysis)

	Y -	y y
K_1 -	911	472
k_1 k_1	302	

1982 W_1 K_1 Y: Genotypes of (K_1 - Y -) F_2 plants
(1982 W_1 - K_1 - Y- F_3-family analysis

Y Y	K_1 K_1	K_1 k_1
W_1 W_1	21	44
W_1 w_1	33	50
w_1 w_1	27	26

Y y	K_1 K_1	K_1 k_1
W_1 W_1	33	59
W_1 w_1	77	131
w_1 w_1	29	70

1981 W_1 T_1 Y: Genotypes of (Y -) F_2 plants
(1981 W_1 - T_1 - Y- F_3-family analysis

Y Y	T_1 T_1	T_1 t_1	t_1 t_1
W_1 W_1	4	6	2
W_1 w_1	10	16	2
w_1 w_1	3	8	4

Y y	T_1 T_1	T_1 t_1	t_1 t_1
W_1 W_1	7	12	12
W_1 w_1	25	16	13
w_1 w_1	10	16	9

Table 3. Tests for random recovery of linkage test alleles[†]

Locus	Year	Population	Classification	Observed incidence	Ratio tested	χ^2 (Probability)	Homogeneity χ^2, df (Probability)
K_1[†]	1981	F_2	Plants; K_1-:k_1k_1	911:302	3:1	0.001 (0.9-1.0)	15.87, 15 (0.25-0.5)
K_1[†]	1982	F_3 from K_1-Y-	Families; K_1K_1:K_1k_1	220:380	1:2	3.000 (0.05-0.01)	-
	W_1K_1Y	F_2 plants	F_2 genotype				
W_1[†]	1981 W_1T_1Y	F_3 from Y -	Families; W_1W_1:W_1w_1:w_1w_1	200:373:202	1:2:1	1.095 (0.5-0.75)	0.779, 2 (0.5-0.75)
	1982 W_1K_1Y	Y-K_1-F_2 plants	F_2 genotype				
T_1[†]	1981	F_3 from Y -	Families: T_1T_1:T_1t_1:t_1t_1	59:74:42	1:2:1	7.469* (0.01-0.025)	-
	W_1T_1Y	F_2 plants	F_2 genotype				

[†]Due to confounding, these tests are for random recovery of alleles; effects of nonrandom vs. nonindependent assortment are not separable in these populations. See text for explanation.

Table 4. Linkage tests*

Independence tested	df	χ^2 (Probability)	Homogeneity χ^2, df (Probability)
K_1-Y -	1	1.815 (0.1-0.25)	-
W_1-Y -	2	4.524 (0.1-0.25)	3.969, 2, (0.1-0.25)
K_1-W_1 -	2	0.472 (0.75-0.90)	-
Y - T_1 -†	2	5.390 (0.05-0.1)	-
W_1-T_1 - †	4	11.060 (0.025-0.05)	-

*Additional tests of linkage are provided by tests of monogenic ratios since only populations segregating for Y y or Y y and K_1 k_1 were grown and classified.

†Expected values adjusted according to overall T_1 t_1 segregation.

Table 5. Comparison of observed assortment to bias expected from linkage effects*

		T_1T_1YY	T_1t_1YY	t_1t_1YY	T_1T_1Yy	T_1t_1Yy	t_1t_1Yy
	Observed	17	30	8	42	44	34
(T_1- adjusted)	expected	19.67	24.67	14	39.33	49.33	28
	deviation	-2.7	+5.3	-6	+2.7	-5.3	+6
Gamete combinations*		CO+	CO+	NCO+	CO+	(NCO+	CO+
		CO	NCO	NCO	NCO	NCO)	NCO
						(CO+	
						CO)	
Calculated frequency of CO products**				0.55 (unlinked)			

*CO = gamete with crossover product, NCO = gamete with non-crossover product; given linkage NCO and CO products should have been excessive and deficient, respectively.

**Maximum likelihood equation solved by iterative approximation, since the pre- and post-differential equations are complex polynomials.

The second test of each linkage combination was a traditional test of independent assortment (Table 4). Because analysis of monogenic T_1 t_1 segregation indicated significantly nonrandom T_1-allele recovery (Table 2), adjusted expectations were used to generate expected frequencies of genotypic classes and, thereby, to obtain unbiased tests of independence for the T_1 locus with Y and W_1 loci.

Nonsignificant χ^2 values for independent assortment were compatible with the hypothesis of nonlinkage between K_1, W_1, and Y loci. Marginally significant and nonsignificant χ^2 values for independence between W_1 and T_1, and Y and T_1 loci were obtained, so data were examined for bias expected if linkage were present. In neither case did linkage explain observed deviations from results expected under the hypothesis of independent assortment. For example, observed deviations in T-Y segregations did not correspond to the directions of deviations expected from repulsion linkage (Table 5). Furthermore, calculated frequencies of cross-over products approximated 0.5 (e.g., 0.55 for T-Y and 0.58 for T-W).

We conclude, therefore, that W_1, T_1, and the Y loci are unlinked, as are W_1, K_1, and Y loci. Our interpretations are compatible with previous assignments of T_1 and W_1 loci to different linkage groups, 1 and 8, respectively. Furthermore, K_1 has not been found linked to alleles of linkage groups 1 or 8.

In summary, the chlorosis described is determined by a single recessive allele. Linkage between the Y locus and K_1, W_1, and T_1 was not detected. We plan to test allelism of this chlorotic mutant with phenotypically similar mutant(s) of the Soybean Genetic Type Collection.

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1) Resistance of soybean cultivars and plant introductions to damage by soybean borer

Due to considerable extending of soybean sowing areas and inculcation of it in new cultivation regions, the losses from diseases and pests are constantly rising. Rich biochemical composition of soybean is an excellent feeding medium for insects and mites, especially its reproductive organs. It is known that more than 500 species of pests parasitize leguminous crops, including more than 90 species of insects and mites.

Soybean borers (*Etiella zinckenella* Tr.) do great injury to soybean. This pest leads to the considerable losses of yield and quality and it is the main pest in this zone, together with the spider mite. The moth of the soybean borer has yellow-grey wings stretched with rusty yellow stripes. Lower wings are light grey with dark piping. Larvae are dirty green with nonclear dark red stripes. Pupae are dark brown and 9-12 mm long. This pest has 2-3 generations annually. Female moths put their eggs on young pods. Larvae of the first generations usually feed on grains of Siberian peashrub, pea and vetch, larvae of the second and third generations feed on soybean and false acacia grains. The biggest reproduction of the pest occurs on false acacia. Little round holes have been seen on injured pods and these pods are less plump and shrunken. Larvae live in the pods about a month, and sometimes migrate from one to another pod. After that they come down onto the surface of soil, transform into pupae and spend the winter in such form.

The possibility of creating pest-resistant forms of soybean has risen significantly in the last ten years in countries where soybean is cultivated, especially in the USA. First of all, there were found the sources of resistance to Mexican bean beetle (Elden et al., 1974; Van Duyn et al., 1971; Van Duyn et al., 1972). The number of adult beetles, eggs and larvae on the resistant forms was very small in the field as it was observed in South Carolina (Turnipseed and Sullivan, 1976). The higher mortality of adult larvae was pointed out when they were feeding on foliage of resistant forms in the laboratory. Their growth and productivity were reduced very much. The forms resistant to Mexican bean beetle (PI 171451, PI 227687 and PI 229358) were tolerant to *Cerotoma trifurcata*, *Heliothis zea*, *Epicauta vittata*, *Pseudoplusia includens* and *Spodoptera exigue* (Turnipseed and Sullivan, 1976). With these forms as a base, some USA states worked out a collective breeding program to create the pest-resistant soybean varieties. Now, there are some breeding lines from crosses of 'Bragg', 'Davis' and 'Forrest' with the donors of resistance mentioned above, which are characterized by resistance to two and more pests (Hatchett et al., 1978). These data show that it is possible to create prospective breeding material with group pest-resistance. The study of inheritance of resistance to Mexican bean beetle shows that it is quantitative (Sisson et al., 1976). Hybrid populations from crosses between resistant and susceptible forms had normal distribution at the third generation. The authors consider that there are two or three major genes affecting resistance level.

Considerable number of studies were made to analyze soybean resistance to corn earworm, *Heliothis zea* Boddie (Joshi and Wutoh, 1976; Joshi, 1977, 1978, 1979). These experiments demonstrated that the three forms resistant to Mexican bean beetle mentioned above were resistant to this pest, too. There were many resistant forms among 2797 plant introductions that were not injured by corn earworm during two and more years. The most resistant were varieties 'Ada', 'Portage', 'Peking', 'Arlington' and others.

Soybean has varietal tolerance to spider mite injury, too (Bailey and Furr, 1975; Carlson et al., 1979).

It is reported that soybeans have been damaged by soybean borer in the conditions of South Ukraine, but limited number of soybean forms were analyzed. Our experiments were made during 1980 and 1981 on fields of "Dachnaya," the base of All-Union Institute of Plant Breeding and Genetics. Soybean samples were sowed at 30-40 m from windbreak plantings of false acacia and Siberian peatree with the aim of creating hard infection background. After maturation, all plants were pulled up and analyzed in the laboratory. All pods of each variety were carefully examined to see if they had been damaged by larvae of soybean borer. The pods without injury were classified according to number of grains in them to simplify calculation of total grain sum. The damaged pods were opened and number of damaged grains was summarized. After that, all data were calculated to amount percentage of damaged pods and grains. In such way, 348 samples were analyzed in 1980, and more than 500 samples in 1981.

The studies showed that damage by soybean borer very much reduced 100-grain weight, sometimes by 60% and more (Table 1). Some grains were fully eaten by pest, others a half or less. Most varieties had losses of 100-grain weight more than 50% as the result of damage (Table 1). When average soybean yield was 2000 kg/ha and level of damage was 10%, then 100 kg/ha of grain had been lost from damage of this pest. Plant introductions from various countries of the world had different levels of resistance to that pest (Table 2). Most had 3-7% injured grains. The main number of forms with less than 1% of injured grains was among Soviet varieties. As a rule, they are Far Eastern breeding. The forms from Japan, USA and China had weak tolerance. For instance, 91 Soviet varieties were studied; 8.8% of them had less than 1% of injury, and 3.3% had level of damage more than 10%. Varieties from USA and China had 3.2 and 12.7% and 3 and 12.1%, respectively. These data show that varieties of Far Eastern breeding have a high level of resistance to soybean borer. Resistant soybean forms are listed in Table 3, and very susceptible varieties are given in Table 4. Varieties K-5776, K-309, 'Amurskaya 401', 'Amurskaya 450', and 'Moneta' had high resistance. The most varieties with high susceptibility to this pest were from USA (Table 4). It must be pointed out that absolute meanings of damage percentage of varieties were different in various years, though their relative levels were in accordance with years. The results of these studies demonstrate that among plant introductions and cultivars of soybean are forms with high resistance to soybean borer. It is important to point out that such high yielding varieties as 'Zarnitsa', 'Belosnejka', 'Severnaya 2', and 'Hodgson' have resistance to this pest and they have complex economical and useful characters. These forms can be used not only as donors of resistance to this pest, but as donors of many other valuable characters, too.

Table 1. The level of soybean grain losses from soybean borer injury

Variety	Weight of 100 grains		Loss percentage
	Undamaged	Damaged	
Ontario	16.5	7.1	57.0
Beechwood	13.9	7.9	43.2
Bukuria	9.9	4.9	50.0
Krasnodarskaya 585	11.1	4.9	55.9
Hybrid 438	10.2	3.9	61.8
K-1187	13.3	9.5	28.6
073-2	13.6	8.5	37.5
Hybrid 646	14.8	5.6	62.2
Peremoga	12.0	6.1	49.2
Lumina	12.4	5.8	53.2
Zora	11.8	5.3	55.1
PI 189995	9.7	3.8	60.8
Nordic 138	11.7	5.9	49.6

Table 2. Distribution of introduction varieties of soybean due to grains damage by soybean borer depending on origin (percent of total amount of tested numbers)

Country	Number of tested varieties	Percent of damage 0-1	1.1-2	2.1-3	3.1-4	4.1-5	5.1-6	6.1-7	7.1-8	8.1-9	9.1-10	More than 10
USSR	91	8.8	4.4	6.6	18.7	5.5	16.5	19.8	7.7	5.5	3.3	3.3
USA	63	3.2	3.2	9.5	11.1	11.1	15.9	7.9	7.9	11.1	6.3	12.7
China	33	3.0	6.1	9.1	15.2	18.2	9.1	9.1	6.1	9.1	3.0	12.1
West and East Europe	30	3.3	10.0	20.0	13.3	3.3	10.0	13.3	3.3	13.3	10.0	0
Canada	10	0	0	20.0	0	20.0	20.0	0	10.0	20.0	0	10.0
Japan	3	0	0	0	0	33.3	0	0	0	0	0	66.7
Others	26	0	0	11.5	15.4	11.5	23.1	7.7	19.2	0	7.7	3.8

Table 3. Soybean forms resistant to soybean borer

		Damage percent			
		of pods		of grains	
Variety	Origin	1980	1981	1980	1981
Amurskaya 411	Far East of the USSR	3.3	4.6	2.4	5.3
Manchu	North China	4.0	0	3.1	0
Severnaya 2	Far East of the USSR	0.5	0	0.3	0
K-5776	North China	0.3	0	0.3	0
K-309	North China	0.2	0.6	0.3	0.5
Pavlikeni 2	Bulgaria	2.7	2.1	2.9	1.7
Varshavskaya	Poland	3.2	2.8	2.5	2.6
Amurskaya 401	Far East of the USSR	0	1.3	0	0.9
K-6334	Brazilia	1.3	1.2	1.0	1.2
Record Severniy	Far East of the USSR	1.6	0.4	0.9	0.5
Herb 620	DDR	0.9	2.4	0.8	2.5
Amurskaya 450	Far East of the USSR	0	1.3	0	1.1
K-4355	DDR	1.2	2.1	0.9	1.4
Hodgson	USA	0.6	3.8	0.3	3.2
Zarnitsa	UkSSR	0.2	1.3	0.1	1.2
Belosnezhka	UkSSR	1.2	2.1	0.9	2.1
Peterson 2090	USA	2.5	0	1.8	0
Moneta	Latvijan SSR	0.2	0.9	0.2	0.8
Amurskaya 147	Far East of the USSR	0.9	3.1	0.5	3.0
Amurskaya yellow	Far East of the USSR	1.3	2.5	0.8	1.3
PI 189863	USA	1.2	0.8	1.2	0.7

Table 4. Soybean varieties highly susceptible to damage by soybean borer

		Damage percent			
		of pods		of grains	
Variety	Origin	1980	1981	1980	1981
Heimkraft	DDR	10.4	22.5	8.8	13.1
Early Hachubu	Japan	24.4	19.2	18.4	17.5
PI 153294	USA	32.5	14.3	25.9	7.8
PI 189995	USA	20.2	11.6	15.1	7.2
PI 153245	USA	35.2	16.8	24.0	12.5
Earlyana	USA	13.8	13.7	9.1	8.4
VNIISK 8012	Krasnodarskij kraj	16.9	10.6	11.8	7.6
K-1286	North China	20.2	10.0	16.8	7.6
K-1657	North China	11.0	19.7	11.3	10.6
Nairn	Canada	18.3	20.7	18.1	18.5
K-434432	unknown	37.8	23.3	20.8	17.8

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2) Activity of trypsin and chymotrypsin inhibitors of soybean forms with different resistance to soybean borer.

In a previous investigation, the wide amplitude of plant resistance of different soybean varieties to soybean borer has been discovered. Our further experiments are directed at the discovery of the main mechanisms of this resistance. It is known that the phenomenon of plant resistance to insects may be classified into three components: nonpreference, antibiosis, and tolerance (Painter, 1951). We use the term nonpreference when the plant is an unfavorable object for feeding and oviposition. When there is antibiosis, the pests have an abnormal biology of development that leads to inhibition of their growth and survival rate and depression of reproductive functions. Tolerance is the capability of plants to withstand damage without particular detriment to the yield.

Results of the study of well-known resistant soybean donors to leaf-feeding pests showed that the resistance was suggesting nonpreference and antibiosis (Elden et al., 1974; Van Duyn, 1972; Beland and Hatchett, 1976; Schillinger, 1976).

Numerous experiments proved that the feeding of different groups of animals on unheated soybean grains leads to the inhibition of their growth and to the appearance of toxicity symptoms. The main reason of this phenomenon is the presence of such antinutritional factors as trypsin and chymotrypsin inhibitors, lectins, phenols and other substances.

Investigations by Jansen and Juster (1976) with *Callosobruchus masculatus* beetle showed that the adding of bean lectins to cowpea meal without this substance leads to a high death rate of larvae. If, in control without lectins, about 4-6 beetles per cowpea grain survived, the addition of 0.1, 1 and 5% of lectins reduced the number of beetles to 3.2, 0.4 and 0,

respectively. With this reason, authors consider that leguminous lectins play an important role in the protection of the grain from the pests.

Since larvae of the soybean borer feed on raw soybean grains, it is very interesting to know the dependence of resistance upon the content of trypsin and chymotrypsin inhibitors.

Activity of the above mentioned inhibitors has been determined by casein method, based the inhibition of casein hydrolysis by trypsin and chymotrypsin (Levitsky, 1979).

Table 1 shows that the content of trypsin inhibitors in mature soybean grains changed significantly (12.6-53.6 mlg/g) depending on varieties. The variability of chymotrypsin inhibitor was significantly lower (14.3-25.3 mlg/g).

Results demonstrated an absence of association between resistance and the activity of inhibitors in soybean grains. Although correlation coefficient with trypsin inhibitors was positive, it had a very low meaning and was not significant (0.24), but it was -0.05 with chymotrypsin inhibitor. For example, varieties resistant to soybean borer (K-4355, 'Peterson 2090', 'Pavlikeni 2') had reduced activity of trypsin inhibitors, while K-4867, K-1390, K-309, 'Zarnitsa' and 'Hodgson' combined high resistance to given pest and increased activity of trypsin inhibitors. The same picture happened to the second type of inhibitor.

As soybean borer is a special pest of leguminous crops, apparently in this case there was the prolonged conjugate evolution of pest and host plants. During this evolution, soybean borer has developed adaptations that play an important role in the feeding on this grain. The normal assimilation of raw soybean grains by larvae shows that trypsin and chymotrypsin inhibitors, present in large quantities in soybean grains, assimilate like other nutrient proteins and don't influence the activity of main digestive enzymes.

It is possible that this pest has several peptide-hydrolases at the first stages of protein proteolysis that are dissimilar from trypsin and chymotrypsin. It isn't out of the question that proteases of soybean borer have some other inhibitors, although they are still unknown.

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Table 1. Content of trypsin and chymotrypsin inhibitors in the seed of different soybean varieties resistant to soybean borer

Variety	% average infected grains	Activity of an inhibitor	
		Trypsin	Chymotrypsin
Amurskaya yellow	1.0	23.6	23.5
Amurskaya 147	1.7	24.2	24.2
Severnaya 2	0.2	30.3	21.7
K-254	7.8	47.5	19.2
K-4355	1.1	20.5	24.6
K-678	1.2	23.6	15.4
K-4867	3.0	53.6	19.7
Hybrid A-6-71	8.9	39.7	18.9
Hybrid 681	10.6	24.2	17.5
Hybrid 467-127	10.0	44.2	18.6
Hybrid 117-9	8.3	40.4	17.2
K-1390	2.7	46.7	16.5
K-309	0.4	52.7	19.7
Hybrid 466-214	2.8	36.7	18.6
Peterson 2090	0.9	12.6	20.0
Pavlikeni-2	2.3	16.7	14.7
Moneta	0.5	25.9	14.3
Virginia	2.4	30.9	14.7
VNIISK 8012	9.7	14.4	18.6
Zarnitsa	0.6	44.6	20.4
Hodgson	1.7	46.2	19.7
PI 153245	18.2	46.7	22.9
PI 189995	11.1	37.2	16.1
K-6468	1.5	29.5	18.4

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VI. ADDENDUM

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1. Evaluation of soybean genetic stock collection from South and Southeast Asia in Himalayan Midhills

With the realization of protein gap in human nutrition and shortage of edible oils in India, great emphasis is being placed on extending the cultivation of soybean in the country. Falling in line with this trend, varieties introduced from the United States of America, e.g., 'Bragg', 'Lee', 'Hardee', etc., were tested in comparison with 'Punjab No. 1', in the midhill region of Himachal Pradesh at Kangra (the place of development of variety Punjab No. 1, evolved in early fifties, Singh et al., 1958), and it was realized that in this region the introductions were not superior to Punjab No. 1 in all the desired agronomic traits (Table 1).

It is known that most of the U.S. varieties have in their ancestry material from Manchuria. Similarly, Punjab No. 1, which is a selection from a Nanking variety (Sikka and Bains, 1952), owes its origin to the Chinese material. This is indicative of a narrow genetic base of soybean material tested so far. It was felt, therefore, that more diverse genetic material should be evaluated for any effort to improve upon the existing soybean cultivars in Himalayan midhills.

With this objective in view, strains from southeastern and far-eastern countries of Asia were obtained through the courtesy of Plant Introduction Division of the Indian Agricultural Research Institute, New Delhi, and evaluated at Kangra. The report of the evaluation is presented in this paper.

Materials and methods: Forty-five cultivars, Indian (17), Chinese (6), Australian (7), Japanese (7), Taiwanese (5) and Nepalese (3) origin of soybean were grown in a test in RBD with 3 replications at Kangra. Three rows, 3 meters long, were sown to each variety. Inter-row distance was kept 75 cm and plant-to-plant spacing was 20 cm, so that each row contained 15 plants. Out of the 3 rows in each cultivar, only the central one was treated as experimental and the border ones were considered as guard rows in order to minimize the intervarietal influence due to competition. Observations on flowering and maturity were recorded on the whole-plot basis, while all other observations were recorded on individual plant basis, from the central rows. For this purpose, five random plants were selected from the central row of each variety in each replication and observations were recorded on plant height, fruiting branches per plant, number of seeded pods per plant, seeds per pod, 100-seed weight and seed yield per plant.

The mean values of the five randomly selected plants in each replication were subjected to the analysis of variance. Genotypic and phenotypic correlations between the traits were worked out. The cultivars were divided in three groups on the basis of yield per plant (Low: up to 15 gms, medium: between 15 to 30 gms, and high: above 30 gms). Similarly, the cultivars were divided into three groups for each trait under study. The frequencies of these character groups were compared for desired character combinations within each yield group.

Table 1. Performance of soybean cultivars introduced from USA in Himalayan midhills

Variety	Maturity period (days)	Plant height (cm)	Branch number/ plant	Seed number/ pod	Pod number/ plant	Seed yield (kg/ha)
Bienville	135	99.7	3.1	1.9	81.4	1943
Bragg	134	90.7	4.3	2.0	83.1	1790
Davis	128	86.2	5.4	2.2	103.1	1950
Hampton	145	86.9	3.9	1.7	97.1	1824
Hardee	145	110.8	4.1	1.9	128.3	2283
Jackson	130	93.8	3.8	1.8	61.9	1925
Pickett	128	79.4	2.5	2.2	68.9	1573
Punjab No. 1	130	91.5	5.3	2.0	109.4	2097
SEm ±	1.102	5.85	0.49	0.141	NS	127.9
C.D. @ 5%	2.29	12.17	1.02	0.293	--	518.0

Results and discussion: The analysis of variance indicated that the varieties differed significantly in all the traits under study (Table 2). The mean and range for almost all agronomic traits indicated that more variability on both extremes is obtainable in the present material as compared to the one introduced and tested earlier (Table 1). In addition to the direct introduction, some of the types would have value as parents for hybridization in improvement programs. The character association in the material would indicate the value of some such types.

Table 2. Range and means of different characters in soybean

Characters	Range	Mean	C.D. @ 5%
Seed yield (gm/plant)	2.67-72.67	25.38	19.44
100-seed weight (gm)	5.00-22.00	12.47	1.45
Seed number/pod	2.00-3.00	2.40	0.29
Pod number/plant	35.00-355.00	123.70	59.72
Branch number/plant	1.00-11.00	6.09	1.35
Plant height (cm)	28.00-184.00	94.90	16.88
Days to maturity	72.00-138.00	111.10	18.52
Days to flowering	30.00-76.00	55.50	10.11

The phenotypic and genotypic correlation coefficients between yield and other agronomic traits are given in Table 3. Significantly positive correlation existed between yield and branch number, pod number, height, flowering and maturity. However, Juneja and Sharma (1971) did not find any correlation between yield and height. Hundred-seed weight had significantly negative association with branch number, plant height, days to flowering and maturity.

On the other hand, pods per plant exhibited significantly positive correlation with the said four traits, which were positively correlated among themselves. Similar associations were observed by Weatherspoon and Wentz (1934), Johnson et al. (1952) and Juneja and Sharma (1971).

The correlations indicate that luxurious vegetative growth (increased height and branch number) resulting from longer growth period (vegetative and reproductive duration) would result in enhanced grain yield. But, for farming totally dependent on rainfall, the breeders' objective would be to have cultivars maturing in less than 120 days, particularly in midhill region of Himachal Pradesh, receiving a total precipitation of above 150 cm during the season and where double cropping is a common practice. Therefore, choice would naturally fall on cultivars combining high yield potential, acceptable seed size and medium to mid-late maturity period. To look for such combinations, 45 cultivars were divided in three groups of low (up to 15 gm), medium (15-30 gm) and high (above 30 gm) yield per plant; each group having a frequency of 11, 19 and 15, respectively. Within each yield

Table 3. Correlation coefficients for some agronomic character pairs in soybean

Characters		100-seed weight	Seed number per pod	Pod number/plant	Branch number/plant	Plant height	Days to maturity	Days to flowering
Seed yield	G[a]	.1375	-.4175	.9652	.7943	.4443	.7112	.6869
	P	.1093	-.1938	.7675*	.5947*	.2623	.2481	.4009*
100-seed weight	G		.0129	-.2550	-.4542	-.4907	-.3940	-.8724
	P		.0890	-.2175	-.4382*	-.4565*	-.2614	-.2847*
Seed number/pod	G			-.2709	.2217	.0811	-.7303	-.1250
	P			-.1346	-.0086	.1115	.0722	-.4271*
Pod number/plant	G				.8515	.5530	.5280	.5906
	P				.7572*	.4426*	.3317*	.7039*
Branch number/plant	G					.7740	.6590	.8306
	P					.6931*	.9680*	.7669*
Plant height	G						.7720	.7272
	P						.6670*	.6642*
Days to maturity	G							.9890
	P							.7626*

[a]G: Genotypic

*Significant at the 5% level.

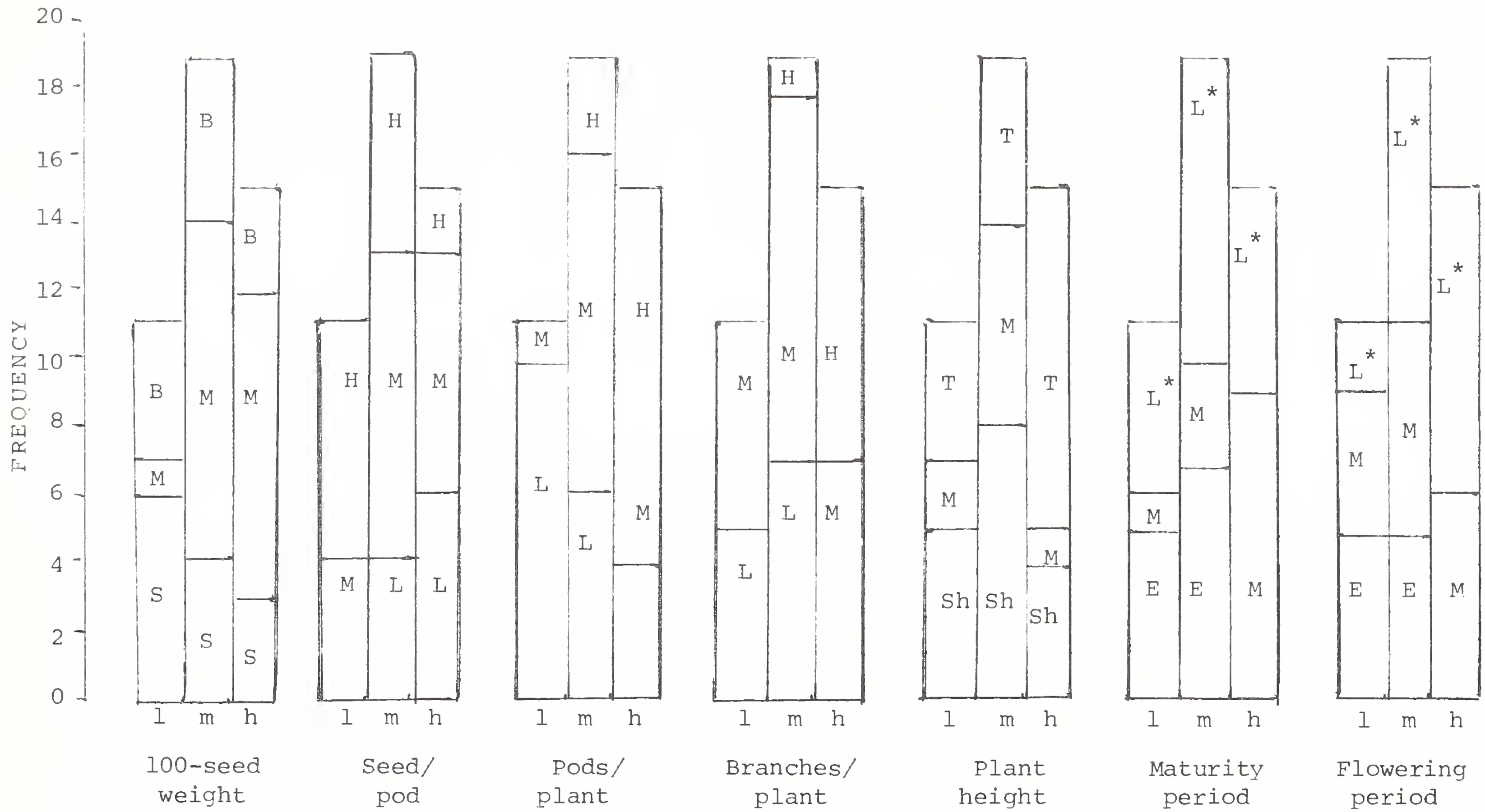

Figure 1. Frequency of soybean types for different traits in three yield groups.

l, m, and h = low, medium, and high yield groups, respectively.
B = bold; E = early; H = high; L = low; M = medium; S = small; T = tall; Sh - short; L* = late.

group, frequency of low, medium and high expression of flowering, and maturity period, growth and yield components were determined. These frequencies have been depicted in Figure 1. A study of this figure reveals that, in spite of certain highly significant correlations, types with medium maturity, medium to bold seed size, and more seeds/pod, exist in the high yield group. The correlations, whether caused by genetic linkages or physiological thresholds, are not absolute, since the frequencies of combinations of characters unlike the indicated correlations are quite high. The grouping also indicates that certain combinations of characters did not exist at all in the present material. For instance, in high yield groups, there were no early flowering or maturing types, nor it had low branching or low podding types. Small, medium and bold seeded types occurred in high yield group in almost the same frequency as in medium yield group. Similarly, though seeds per pod had negative correlation with yield, types with high seed number existed in high yield group.

Correlation coefficients and grouping of frequency distributions jointly provided clearer picture of desirable character combinations in the genetic stock collection studied and it should be possible, with the present material, to select or breed types superior to Punjab No. 1, which is an ace variety, even after 2 decades of its evolution.

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